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ONTARIO RESEARCH ENHANCEMENT PROGRAM (O R E P)

Final Report

INCREASING NITROGEN USE EFFICIENCY IN CORN PRODUCTION SYSTEMS: QUANTIFYING EFFECTS OF QUALITY OF SOIL STRUCTURE AND WATER REGIMES

REPORT No. OREP - 1999/12

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Canada

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FORWARD

The Ontario Research Enhancement Program (OREP) is a $4-million two-year federal research initiative that is administered by the Research Branch of Agriculture and Agri-Food Canada (AAFC), with input from the agriculture and agri-food sector, universities and the province. Research focuses on two areas identified by the sector as:

1. Priorities responding to consumer demand for higher quality products; and
2. Ensuring crop-production management systems are environmentally sustainable.

Biotechnology is one of the areas to be explored. Ontario's agricultural production is based primarily on growing diversified crops using intensive production practices, but long-term viability is linked to the development of sustainable crop production management systems.

There are also opportunities to enhance the economic contribution of Ontario's agriculture and agri-food sector by adding value to the diversified primary commodities produced in the province. The Program is expected to be of particular interest to the corn, soybean, greenhouse, fruit and vegetable sectors and the emphasis will be on projects focussing on food quality improvement and sustainable crop production management such as:

1. The development of value-added animal and crop food products and ingredients that meet domestic and export market demands, with a particular emphasis on quality issues such as processing, packaging, shelf life, new product and ingredient development, high-value alternative uses, probiotics and functional foods;
2. Biotechnologies to reduce environmental pressures related to crop protection practices; and,
3. Integrated crop protection and production practices for both field and greenhouse crops.

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Executive Summary

The primary objective of this research was to develop measures of the quality of soil structure for the mineralization of organic-N and for the uptake of mineral-N by corn. The long term goal is to use measures of the quality of soil structure and water regimes, in conjunction with measures of potentially available N, to develop more accurate recommendations for fertilizer-N applications and thereby increase nitrogen use efficiency. An additional goal (not directly related to this project) is use these measures to define yield potentials and subsequently help interpret the variability in yields across landscapes.

Plant and microbiological response to varying water contents in soils of different structure were used to define measures of the quality of soil structure. This approach is in marked contrast to most previous studies in which soil structure has been defined solely on the basis of physical measurements. Plant response was characterized, in controlled environments, using gas exchange measurements (photosynthesis and transpiration). Gas exchange was found to be strongly positively correlated with N uptake. Microbiological response was characterized using measurements of net N mineralization after incubating the soil under controlled environment with and without an amendment of red clover residue. Use of plants and microorganisms to define measures of the quality of soil structure introduce the possibility that the measures may be influenced, in the case of plants, by hybrid and stage of development and, in the case of microorganisms, by the stage of decomposition. Consequently, measurements with plants were made at different stages of plant development (early vegetative, 6-leaf; late vegetative, 12 or 15-leaf; silking and grain-filling) and two different hybrids (Pride 5, introduced in Ontario in 1959 and Pioneer 3902, a more recent hybrid introduced in 1988). Net N mineralization was measured after two different incubation periods (1 and 3 months). Different structural characteristics were obtained by using soils with clay contents ranging from 5 to 41% (10 soils) that were compacted to two different levels. Different water regimes were established for the plants by growing them under optimum conditions and then either withholding water and allowing the soils to desiccate, or adding water and progressively increasing the water content to saturation. Water regimes for the microbiological studies consisted of maintaining the water contents at values equivalent to different proportions of the pore space filled with water. A preliminary field study was conducted in 1998 to assess the applicability of the results from studies in controlled environments to those under field conditions.

Gas exchange in plants is often considered to follow a curvilinear relation with water content, with rates of exchange declining at low water contents due to low water potential and/or high soil resistance to root penetration and at high water contents due to lack of aeration. The approach used to define measures of the quality of soil structure for plant

growth was to define a range in water contents that were non-limiting to gas exchange (transpiration or photosynthesis remained constant as water contents varied across this range), and a range in which gas exchange approached zero at both the upper and lower limits of the range. It is normally assumed that gas exchange will be the same in soils with different structural characteristics if the water content is in the non-limiting range.

Gas exchange rates varied as soils dried from the optimum water content and critical water contents representing the lower limits of both a non-limiting water range and a least limiting water range were defined for each soil. These limits did not vary with the gas exchange measurement (whole plant transpiration, leaf transpiration, leaf photosynthesis) or hybrid but did vary slightly with stage of development. The critical water contents were strongly correlated with clay and organic carbon contents but, surprisingly, could not be related to characteristic values of water potential or soil resistance to penetration.

A critical water content could not be identified for gas exchange in plants as soil water contents increased to saturation. Gas exchange rates did not immediately respond to increasing water content above that of the control, in contrast to measurements made under drying conditions. The oxidation state of the soil (as measured by redox potential) declined progressively over time when the soil was saturated. The response of plants to declining oxidation varied with the stage of development. Rates of gas exchange of plants at the silking and grain filling stages were not influenced by saturating the soil for 10 days. At the 15-leaf stage, the impact of saturating the soil on gas exchange was time-dependent and gas exchange rates only began to decline once the redox potential had reached threshold values. Up to 6 days were required before the threshold redox potential was reached and the threshold values varied with soil and hybrid. While the results of these studies raised a multitude of questions regarding variation in the response of different hybrids on different soils to water logging that merit further study, the studies did not identify a critical water content that could be used as an upper limit for either the non-limiting or least limiting water range.

Evidence was not found to support the commonly held assumption that rates of gas exchange, plant development and N uptake are the same for plants growing in soils with different structure when the water content is in the non-limiting range. Instead, gas exchange rates, rate of plant development and N uptake were found to vary among soils and were strongly negatively correlated with clay content. The mean weight diameter of aggregates was positively correlated with clay content which resulted in a strong negative relation between aggregate diameter and gas exchange rates, rate of plant development or N uptake. Although the reason(s) for these relations were not identified, the relations have profound implications with respect to yield potentials and the crop response to reduced tillage in fine textured soils, if the results apply to field conditions. Further research is necessary to investigate this possibility.

Nitrogen mineralization is normally quadratically related to water content or water-filled pore space (WFPS), declining at low water contents due to low water potential and at high water contents due to inadequate aeration and subsequent denitrification. Consequently, there was not a range in which water contents were non-limiting to net N mineralization. N mineralization increased over time (i.e. from one to three months) for all compaction and legume treatments. Legume addition increased N mineralization especially at WFPS values ranging from 50 to 65%. Critical water contents for net N mineralization were identified. The lower critical water content coincided with the water content at which there had been no net increase in inorganic N above the initial level after incubating soil for 1 or 3 months. This limit was found to be similar or lower than the critical water content at which gas exchange in corn approached zero. This implies that the demand for N by the crop would reach minimum values (assuming the variation with soil water content in plant growth and N demand parallel that of gas exchange) at water contents equivalent to, or greater than that at which net N mineralization is zero. The upper critical water content coincided with the water content at which denitrification reduced the inorganic N level to the initial level after incubating soil for 1 or 3 months. The upper critical water contents increased with soil compaction and duration of incubation. The upper limit was less than the water content at field capacity in several soils indicating that significant losses of N would occur in these soils, through denitrification, after rapid drainage had ceased.

In the absence of a well-defined upper limit of water contents for gas exchange, the upper limit for net N mineralization was used in conjunction with the lower limit for gas exchange to define a least limiting water range (LLWR) for plant growth. This estimate of the LLWR implies that plant growth at the lower end of the range is limited by physical constraints (water supply or soil resistance to penetration) and at the upper end by inadequate N supply. The LLWR varied parabolically with clay content and, at low clay contents, increased with organic carbon.

The most extensive drought occurred during the silking period in the preliminary field study. Stress experienced by the crop in that period was expected to have had a strong influence on final grain yield. Non-linear regression techniques were used to relate yields to soil water content at that time and critical water contents calculated in a similar manner as that used in the gas exchange studies in the growth rooms. The critical limit at which yields approached zero was similar in magnitude to that at which gas exchange approached zero under growth room conditions. The field study also confirmed results found in the growth room study showing that the critical water contents did not vary with hybrid.

The study demonstrated the utility of characterizing the structural quality of soils using least limiting water ranges derived from a combination of plant-derived gas exchange

measurements and measurements of net N mineralization. The next stage of this research is to evaluate the critical water contents of soils under field conditions. The evaluation should include measurement of the critical water contents in different soils and an assessment of the accuracy of the regression equations to predict least limiting water ranges from texture, organic carbon and relative compaction.

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1. Introduction

Inorganic nitrogen (N) fertilizer is an essential component in the production of corn and makes up > 20 % of the operating expenses. However, N not used by the crop can also be a source of nitrous oxide (a greenhouse gas) and is a potential pollutant of groundwater. The profitability is greatest and the environmental costs least when the nitrogen use efficiency (NUE) is maximized. The NUE is determined by two sets of factors: those controlling the amount of inorganic-N in the soil and its variation over time, and those controlling both the uptake efficiency of N by the crop (plant-N per unit soil-N) and the utilization efficiency (grain yield per unit plant-N). Mineralization of organic-N from crop residue and soil organic matter can provide 30-100% of the crop requirements with the largest amounts being provided when either direct or underseeded forage legumes precede the corn crop. Both the microbiological processes responsible for mineralization of organic-N and the biological processes responsible for plant growth and yield are strongly influenced by soil structure and soil water content.

Soil structure and water content vary with soils and tillage practices, and can vary spatially and temporally within a field. NUE of a crop will be maximized when the rate of mineralization of organic-N is synchronized with the uptake of N by the crop. However, the degree to which the amounts of N mineralized from organic sources can be synchronized with the uptake of N by corn in soils that have different structural characteristics and soil water regimes is unknown.

The research approach that has been used in this project was based on the hypothesis that fertilizer-N requirements of a hybrid (or class of hybrids) of corn can be predicted from a soil test for N that is potentially available, and which can be adjusted for: (i) the quality of soil structure and water regime for the mineralization of residue-N, and (ii) the quality of soil structure and water regime for corn growth and N uptake. These adjustments would account for the influence of soil conditions on the degree of synchronization between mineralization and uptake of N. The first task in testing this hypothesis was, therefore, to develop a measure of the quality of soil structure and water content for N uptake when N was not limiting and a measure of the quality of soil structure and water content for the mineralization of organic N when this is the primary source of N for the plants. Since the measures of the quality of soil structure for N uptake were necessarily based on plant parameters, a supplementary task was to determine if the measures varied with hybrid or stage of development.

2. Objectives

The objectives of the study were to:

- develop a measure of the quality of soil structure and water regime for uptake of N by corn, and for the mineralization of residue-N and,
- complete a preliminary evaluation of these measures using data obtained from existing field trials.

3. Organization of report

Studies on plant growth and N uptake are reported under conditions when soil water content was considered to be non-limiting (chapter 4) and when the water content was declining and either water potential and/or soil resistance to penetration became limiting (chapter 5). The influence of hybrid and stage of development is next considered under conditions when water was non-limiting, when the soil was drying and when soils were water-logged and therefore soil aeration was limiting (chapter 6). Studies on the influence of soil structure and water content on net N mineralization leading to a definition of a least limiting water range for mineralization are reported in chapter 7. The material from these studies is then used to define a least limiting water range for plant growth and N uptake (chapter 8). The applicability of the results from these studies to field conditions are then assessed in a preliminary field study (chapter 9). Finally, an overall summary of the study and recommendations on future directions in research are presented in chapter 10.

4. Variation in plant growth, development and N uptake efficiency in soils of different structure under "non-limiting" water contents.

4.1. Introduction

Soil texture, soil organic carbon (OC) content, and the extent of soil compaction have a dominant effect on soil structure and on the variation in soil water content through the growing season. Consequently, it is reasonable to base studies on the development of measures of the quality of soil structure and water content for plant growth and N uptake on soils differing in texture, OC content and extent of compaction.

Soil structure and water content are believed to influence biological processes related to plant growth (e.g., rate of transpiration and photosynthesis, biomass accumulation) by imposing limitations on the supply of oxygen, the availability of water and the soil resistance to root penetration (Letey 1985). Although there is no information on the impact of soil structure and water content on the rate of plant development or on N uptake efficiency, there is no reason to suspect that these processes would be influenced differently from others. If oxygen supply, availability of water and soil resistance are the only limiting factors, plant behavior would be expected to be similar in soils of different texture, OC content and relative compaction, providing the soil water contents are in a range that none of these factors are limiting. There are, however, isolated reports in the literature of the early shoot and root growth of maize (Zea mays L) changing with structural characteristics when water and nutrients were not considered to be limiting. For example, Donald et al. (1987) and (Alexander and Miller 1991) varied structural conditions by selecting aggregates of different sizes from a loam-textured soil and found shoot weight decreased as aggregate diameter increased. The proportion of fine roots and the total root length was greater in the beds of finer aggregates. Alexander and Miller (1991) found that the shoot : root ratio declined with increasing aggregate size and that the response of maize to varying aggregate size was rapid reaching significant levels as early as 8 days after emergence. Although the authors were unable to identify a characteristic of the aggregate beds to which the plant roots were responding, or to identify the physiological mechanisms involved in the response, their studies introduce some uncertainty in the expectation that plants behave similarly in soils of different texture, OC content and relative compaction providing water and nutrients are not considered limiting.

4.2. Objectives

The objective of this study was to determine the influence of soil texture, soil organic carbon content, and the extent of soil compaction on transpiration, photosynthesis, N uptake efficiency, shoot growth and plant development of maize (Zea mays) under non-limiting soil water conditions.

4.3. Materials and methods

Samples of eight soils, collected from the A horizon of fields that had been conventionally tilled (ploughing in the fall or spring followed by secondary tillage in the spring) and under either a corn/soybean/wheat or corn/soybean rotation for several years were used for the study. The soils represented a range in textures and OC contents but were similar in pH and mineralogy (dominantly poorly weathered micas). Soils were purposely selected such that there was no correlation between clay and OC contents and therefore the impact of these two variables could be assessed independently. The soils were air-dried, sieved (<6 mm) and analyses of texture, OC content, and chemical properties completed. The reference bulk densities were determined when drainage ceased after compacting saturated samples of the soils at 200 kPa (da Silva et al. 1997). The water release curve was determined for each soil at its respective bulk densities (Klute 1986); and the soil resistance to a cone penetrometer (30° angle) was measured as a function of water content (da Silva and Kay 1997). Selected characteristics of these soils are given in Table 4.1.

Nutrients were added to the soil and then the soil packed in 6 L plastic pots to a relative compaction (Häkansson 1990) of 0.83 or 0.91. These values of relative compaction represent values commonly found under conventional till (0.83) and no-till (0.91) across a range of soil textures, OC contents and climates (Kay et al. 1997). The bulk densities (Table 4.1) appropriate for each soil and compaction treatment were then calculated by multiplying the reference bulk densities (Table 4.1) by the relative compaction, and the amount of soil required to fill a volume of 5.13 L in a pot at the required bulk density determined. Nutrients, in the form of dry reagent grade chemicals (NH_4NO_3, $Ca(H_2PO_4)_2*2H_2O$, and K_2SO_4) were mixed with the soil weighed for each pot. Nutrients were added to the soil at rates of 2.5 g N per pot, 150 mg P per kg soil and 50 mg K per kg soil (P and K were added on a unit soil weight basis recognizing that these nutrients are more reactive with the soil than N and the pots contain different weights of soil). Four additional drainage holes were drilled at the base of the side of the 6 L plastic pots and the soils were packed in the pots to the required bulk density in 3 cm depth increments. Pots were then wet from the base to saturation with distilled water and submerged for 1-3 days (depending on texture). The pots were then removed from the containers in which they were saturated, covered with plastic to prevent evaporation, and

allowed to drain until there was no further water loss. The equilibrium water content (normally achieved with 2 days) was referred to as the free drainage limit (FDL). Additional pots that were packed at the same time, saturated and drained in a similar manner were used to assess the uniformity in packing and to determine dry aggregate size distributions. No statistically significant variation in bulk density was found on sampling radially or with depth in the pots. Air-dried soil from the pots was shaken on nested sieves by hand for 1 min. and the oven-dry weight of soil on each sieve (<0.075, 0.075-0.50, 0.50-1.0, 1.0-2.0, 2.0-6.0 mm) used to calculate the mean weight diameter of the aggregates.

The experiment was laid out as a randomized complete block design with 8 soils, 2 levels of relative compaction, 2 wetting treatments (a control and a drying treatment) and four replications. Each replication was contained in 2 growth cabinets in which the 32 treatments were randomly assigned. The control is discussed in this chapter and the drying treatment discussed in the following chapter.

A short-season hybrid Pioneer 3902 was used in this experiment. Pioneer 3902 was introduced in 1988 and was one of the most widely grown hybrids during the 1990's in central Ontario (Tollenaar 1994). Seeds were placed in a solution of 50% of bleach and 50% of water, stirred for 15 min to sterilize, rinsed thoroughly with deionized water, and then soaked in an aerated baker 48 hr for pre-germination. Prior to sowing, seeds were immersed in a 2% solution of Benelate, a wettable fungicide powder containing 50% Benomyl (Dupont Canada Inc.) for 20 min to prevent Fursarium infection. Three pre-geminated seeds were planted to each pot and seedlings were thinned to 1 plant at the 3-leaf stage. Two hundred g of sand was used to cover the pot surface to minimize evaporation and soil crusting. Plants within a growth cabinet were periodically rotated to minimize plant-to-plant variability.

The experiment was conducted in controlled-environment growth cabinets (Model PGW36, Controlled Environments, Winnipeg, Manitoba. Growth conditions were 26/16 °C day/night temperature, with a 16-h photoperiod, and a relative humidity of approximately 75%. The photosynthetic photon flux density (PPFD) was maintained at approximately 650 μmol m^{-2} s^{-1} at the top of the canopy, with a mixture of 'cool white' fluorescent tubes and 'inside frost' tungsten bulbs (Osram Sylvania, Drummondville, Quebec). Air temperature in each growth cabinet was continuously monitored with thermocouples placed closely to the whorls of four plants.

Pots were weighed twice a week at the beginning of the growing period and weighing increased in frequency to daily measurements by the 12 leaf stage. The amount of water required to return the volumetric water content to that equivalent to an air-filled porosity (AFP) of 10% (volume air-filled pores/total soil volume) was calculated from the pot weight, the weight of oven dry soil in each pot, the volume of the soil, the density of water and the

estimated fresh weight of the plants. Adjustments for plant fresh weight at different leaf stages and days after sowing was estimated according to previous maize physiological studies (Tollenaar and Migus 1984, Tollenaar 1989, 1999).

The time elapsed from emergence to the 12 leaf stage (the 12th leaf was visible in the whorl) was taken as a measure of the rate of plant development. Once the plants reached to 12-leaf stage, measurements of transpiration and photosynthesis were initiated. The pots were completely enclosed in white plastic bags and the bags tightened around the base of the stem to prevent soil evaporation. The pots were weighted every night between 20:00 and 21:00 hr. and water added to return the water content to that equivalent to 10% air-filled porosity. This timing maximized the opportunity for water redistribution in the pots prior to the start of the next light period. Transpiration was measured on a whole plant basis and on a unit leaf area basis (in conjunction with photosynthesis measurements). Whole plant transpiration measurements were based on the difference in pot weight on successive days minus the plant weight increase. Leaf photosynthesis at 650 μ mole m^{-2} s^{-1} was measured using a portable, open-flow gas exchange system LI-6400 (LI-COR Inc., Lincoln, NE). Measurements were taken on the youngest, fully expanded leaf at 13:00-15:00 p.m. for all treatments. Exchange of CO_2 between the leaf sample and the measuring chamber air was measured for a 6-cm^2 area of the leaf, excluding the midrib. The flow rate of air through the chamber and sample side of the infrared gas analyzer was set to the 500 μ mole s^{-1} in order to minimize the system response time to a change in photosynthesis. The CO_2 concentration of the intake air was maintained at 350 ppm using the 6400-01 CO_2 injector (LI-COR Inc. Lincoln, NE). Leaf temperature was maintained at 26 ± 1 °C by the LI-6400's Peltier thermoelectric coolers. All photosynthesis and leaf transpiration rates were calculated by the LI-6400's operating software, which follows the method of von Caemmeerer and Farquhar (1981). Above-ground plant material (shoot) was harvested, dried at 80 °C to constant weight and the concentration of major and minor nutrients determined. Nitrogen use efficiency was expressed as total N in above-ground biomass divided by N added.

4.4. Results and discussion

The statistical characteristics of shoot dry weight, time to 12 leaf stage, whole plant and leaf transpiration rates, photosynthesis rates and nitrogen uptake efficiency are given in Table 4.2. Simple linear correlations between these plant parameters and soil properties (textural characteristics and their squared terms, OC and OC^2, relative compaction) were determined and properties that were significantly ($P \leq 0.05$) related to a plant parameter then used in forward stepwise multiple regression analyses (Statsoft 1999) to identify the soil variables most strongly correlated with the plant characteristics. These analyses (Table 4.3) identified only percent clay or $(\text{percent clay})^2$ from among the soil variables as being significantly correlated with the plant parameters (all coefficients were significant at $P \leq 0.05$). The relation between one of these plant parameters (photosynthesis rate) and clay content is illustrated in Fig 4.1. It is of interest to note that neither relative compaction nor bulk density were selected in the analyses. This may mean that the range in relative compaction (0.83 to 0.91) was not large enough to influence plant parameters under growth room conditions.

Increasing clay contents can lead to decreasing aeration at high water potentials and have also been related to decreasing availability of water (Kay et al. 1997), and increasing soil resistance to penetration (da Silva and Kay 1997). Any one of these factors would be consistent with the decline in shoot weight, rate of development to the 12 leaf stage, photosynthesis, and transpiration rate, that was observed with increasing clay content. Limited aeration would be expected to be related to low air-filled porosity, low redox potential and elevated concentrations of Mn. However, none of the measurements of these characteristics provided any evidence of limited aeration in this study. The daily average air-filled porosity, during the period that transpiration and photosynthesis measurements were made, varied from 0.11 to 0.18 with a mean value across all soils of 0.14. The average air-filled porosity, under the conditions of this experiment, did not vary with clay content (primarily because the water content was returned to that equivalent to an air-filled porosity of 10% at the end of each transpiration period). Redox potentials were measured twice during the period that transpiration and photosynthesis measurements were made by inserting a combination platinum and calomel electrode about 1 cm into the soil at the surface of the pots (data not reported). The measurements did not reveal any statistically significant variation of redox potential with textural variables or relative compaction. The average potential was +406 mv, which is indicative of a well aerated environment. Subsequent studies (chapter 6) showed that gas exchange only began to decline when the redox potential fell below about 240 mv. Finally, Mn concentrations were lowest in the soils with higher clay contents. These soils would have been most susceptible to aeration limitations and, under anaerobic conditions, the concentration of Mn in the soil solution would have increased.

The relatively low transpiration rates (in comparison with transpiration rates under field conditions) would be expected to result in the soil water potential adjacent to the plant roots being similar to the potential throughout the pot. The water potential at the average daily water content of each pot was calculated from the water release curves for the 16 soils. The variation in potential between soils did not provide any evidence of limitations due to water potential. Although the water potential decreased slightly with increasing clay content and increasing relative compaction, values only varied from 0.0024 to 0.015 MPa with an average value of 0.008 MPa. The water potential at the average daily water content was not correlated with shoot weight, time to the 12 leaf stage, photosynthesis , leaf transpiration rate or whole plant transpiration rate. Furthermore, no decreases were observed in either leaf transpiration rate or photosynthesis when the water was withheld from the plants (reported in the next chapter) until the water content declined beyond a critical value corresponding to a potential averaged across all soils of 0.064 MPa.

Increasing soil resistance to penetration has been reported to cause a decrease in shoot growth and in transpiration rates when water potential was not limiting (Masle and Passioura 1987). The soil resistance to penetration at the average daily water content was calculated from the soil resistance curve (soil resistance to penetration versus water content) for each soil and was found to vary from 0.02 to 1.08 MPa with a mean of 0.55 MPa. The soil resistance at the average daily water content was positively correlated with clay content and relative compaction (R^2=0.82) in a forward stepwise regression. When forward stepwise regression analyses were applied to the plant parameters (shoot weight, time to 12 leaf stage, photosynthesis rate, and leaf and whole plant transpiration rates) as dependent variables and potentially limiting soil properties (soil resistance, water potential, air-filled porosity and redox potential) used as independent variables, only soil resistance to penetration was selected in statistically significant relations for each of the plant parameters. The relationship between one of these plant parameters (photosynthesis rate) and soil resistance to penetration is illustrated in Fig 4.2. Although these relations are compatible with the observations of Masle and Passioura (1987), soil resistance accounted for 0.5, or less, of the variability in the different plant parameters. An additional reason to suspect that soil resistance was not primarily responsible for the reduction in the plant parameters at the large clay contents was reflected in the observation that the soil resistance in each soil increased with decreasing water content when water was withheld from the plants (reported in the next chapter), but there was no decrease in rates of photosynthesis or transpiration until the water content fell below a critical value. The soil resistance, at the critical water contents, averaged across all soils had, however, increased to 1.7 MPa (an increase by a factor of 3 above that observed for the control). It is not obvious, therefore, how an increase in soil resistance across soils under the control conditions could cause a decrease in transpiration and photosynthesis, but not cause a reduction in transpiration or photosynthesis in

any of the soils when the soil resistance was increased in each soil due to a decrease in water content.

The variation in nitrogen uptake efficiency with clay content was unexpected. However, an examination of the concentration of N in the plant tissue (Table 4.4) shows that the values did not vary uniformly with clay content; the concentrations of N were lower in soils with clay contents ≥27% than in soils ≤15%. Similar trends were obvious, though less pronounced, with P, Ca, Mg and Mn (significant negative correlations with clay content were obtained for each of these nutrients). Concentrations of K,Cu, Zn and B did not vary with clay content. The concentrations of N, P and Mg with clay contents ≥27% were at or below values considered to be critical at silking (Jones and Eck 1973). Since shoot weights also declined with increasing clay content, expressing nutrient levels on a whole shoot basis accentuated the trends in tissue concentrations (Table 4.4). Although the nutrient contents in the soil were not measured at the end of the experiment, N, P and K were added to soil at the beginning of the experiment in amounts considered to be more than adequate to meet plant requirements. The possibility of inadequate levels of soil nutrients contributing to the low tissue concentrations in the soils with ≥27% clay is further discounted when the tissue concentrations of elements not added to the soils (Table 4.4) are compared to levels in the soil (Table 4.1). For instance, there is no correlation between concentrations of Ca in shoot tissue and the levels of Ca in the soils. The data suggest that the capacity of the roots to take up nutrients was substantially lower in soils with clay contents ≥27%. The decline in shoot weight, days to 12 leaf stage, photosynthesis rate, and leaf and whole plant transpiration rates with increasing clay content may be linked to the lower nutrient uptake at higher clay contents. When tissue nutrient concentrations were included among the independent soil properties in stepwise multiple regression, nutrient concentrations (particularly %N) replaced soil resistance to penetration in the regression equations for all plant parameters and were the only variables selected. The relation between one of these plant parameters (photosynthesis rate) and %N is illustrated in Fig 4.3. Photosynthetic rate linearly increased with increasing of leaf N concentration up to approximately 3%. Positive linear relationship at lower leaf N levels and asymptotic relationships at higher leaf N levers have been also reported in several studies (Goudriaan and van Keulen, 1979; Sinclair and Horrie, 1989; van Keulen et al., 1989). Similar results were also reported in wheat (Schmidt et al., 1981) and rice (Peng et al., 1995). Higher leaf N increased the phosphoenol pyruvate carboxlase enzyme level, which is the principal corn carbon fixation enzyme and represents 20-35% of the leaf soluble protein (Brown, 1978), subsequently, increased the photosynthetic rate. Donald et al. (1987) found that the uptake of several nutrients were reduced as aggregate size increased (and shoot weight declined). Although the magnitude of the decreases were smaller than those observed in this study in soils, with higher clay contents (Table 4.4), the decreases observed by Donald et al. (1987) were significant for

Ca, Mg, Mn, Zn and B. No decrease was observed for N or P. The mean weight diameter of aggregates in the soils used in this study increased with clay content (Fig. 4.4). Increasing aggregate size was also negatively correlated with tissue nutrient concentration of N, P, and Mn (the variation in the content of N and P with mean weight diameter is illustrated in Fig. 4.5). Shoot weight, rate of development, as well as rates of photosynthesis and transpiration were also negatively correlated with the mean weight diameter of aggregates (the variation in the rate of photosynthesis is illustrated in Fig. 4.6). The reduction in shoot weight with increasing aggregate size was similar in this study to that observed by Donald et al (1987) and Alexander and Miller (1991). For instance, a reduction in shoot weight in the larger aggregates (>1.6 mm) compared to the smaller aggregates (<1.6 mm), as a fraction of the shoot weight in the small aggregates, of 0.23 was observed by Donald et al. (1987). The fractional reduction in shoot weight for soils with clay contents ≥27% (corresponding to aggregates with a mean weight diameter ≥1.3 mm) was 0.26. However, in contrast to the data obtained in this study, neither Donald et al. nor Alexander and Miller observed any reduction in transpiration rates with increasing aggregate size. It is of interest to note that they also did not observe any decrease in N uptake.

Although intriguing similarities exist between the observations in this study and those of Donald et al. (1987) and Alexander and Miller (1991), one would expect much greater variation in the characteristics of the aggregates in this study than in the other two. For instance, the aggregates used by Donald et al. and by Alexander and Miller came from the same soil. Alexander and Miller found that the clay content of the different aggregate size fractions only varied from 18.0 to 21.0%. This may mean that the high clay contents accentuate the effects of larger sized aggregate in this study and account for discrepancies between the studies, particularly those related to the uptake of N and transpiration rates. Depending on the nature of aggregation, the intra-aggregate pore space may be completely anoxic while inter-aggregate pores are well aerated (Horn et al. 1994). Renault and Sierra (1994) have modeled oxygen diffusion in aggregated soils and shown that the anaerobic fraction is very sensitive to aggregate size. Recent calculations based on fractal models of soil structure (Rappoldt and Crawford 1999) suggest that, at a given air-filled porosity, the anaerobic fraction increases with decreasing mass fractal dimension. Rasiah et al. (1993) showed that the mass fractal dimension of aggregates was negatively correlated with clay content. An analysis of the curves presented by Renault and Sierra (1994) for soils with a bulk density of 1.1 Mg m^{-3}, suggest that at the air-filled porosity corresponding to the average value of the pots in this study, the anaerobic fraction of soils could vary from 0.03 to 0.31 as aggregate size increased from 1.25 to 5 mm. If these calculations apply to our study, it would mean that the redox potentials measured near the surface of the soil either did not represent the potentials that existed throughout the pots or were not sensitive to the potentials existing within aggregates. However,

data on the upper limit of the water contents for zero net N mineralization, presented in chapter 7, do not provide evidence that aeration may have been sufficiently limiting as to result in a net loss of soil N through denitrification in the soils with high clay contents. Further studies are necessary to assess the possibility that spatially variable anaerobic conditions contributed to the response of plants to the variation in clay content that was observed.

Nitrogen was added to the soils at a single rate in this study. We cannot, therefore, determine if shoot weight and rates of transpiration and photosynthesis in the soils with clay contents ≥27% could be increased to those of the other soils by employing higher N application rates. This possibility will also have to be examined in future research.

4.5. Conclusions

Shoot weight, days to 12 leaf stage, photosynthesis rate, and leaf and whole plant transpiration rates declined with increasing clay content. There was no evidence that the decline in these plant parameters with clay content was due to decreasing aeration, decreasing water potential, or increasing soil resistance to penetration. Nitrogen use efficiency was less in soils with clay contents ≥27% than was the case for soils with clay contents ≤15%. The concentrations of P, Ca, Mg and Mn in the shoot tissue were also less in soils with the greater clay content. Although the lower uptake of nutrients at the larger clay contents may have contributed to the behavior in the other plant parameters, the causes of the reduced nutrient uptake at larger clay contents are not clear. Aggregate size was positively correlated with clay content and the variation in shoot weight and the uptake of some nutrients with aggregate size was similar to that reported by Donald et al. (1987) and Alexander and Miller (1991). However, the causal mechanisms that are involved were not identified.

4.6. References Cited

Alexander, K. G., and M. H. Miller. 1991. The effect of soil aggregate size on early growth and shoot-root ratio of maize (*Zea mays* L.). *Plant Soil* 138: 189-94.

Brown , R. H. 1978. A difference in nitrogen use efficiency in C3 and C4 plants and its implications in adaptation and evolution. *Crop Sci.* 18:93-98.

da Silva, A. P., and B. D. Kay. 1997. Estimating the least limiting water range of soils from properties and management. *Soil Sci. Soc. Am. J.* 61: 877-83.

Häkansson, I. 1990. A method for characterizing the state of compactness of the plough layer. Soil and Tillage Research. 16:105-120.

Donald, R. G., B. D. Kay and M. H. Miller. 1987. The effect of soil aggregate size on early shoot growth and root growth of maize (Zea mays L.). *Pant Soil* 103: 251-259.

Goudrriaan, J., and H.van Keulen. 1979. The direct and indirect effects of nitrogen shortage on

photosynthesis and transpiration in maize and sunflower. Neth. J. Agric. Sci. 27:227-234.

Häkansson, I. 1990. A method for characterizing the state of compactness of the plough layer. *Soil and Tillage Research.* 16:105-120.

Horn, R., H. Taubner, M. Wuttke, and T. Baumgartl. 1994. Soil Physical Properties Related to Soil Structure. *Soil Till. Res.* 30: 187-216.

Jones, J. B., and H. V. Eck. 1973. Plant analysis as an aid in fertilizing corn and grain sorghum. *In* Soil testing and plant analysis. Rev. ed. Eds. L.m Walsh and J. D. Beraton. 491 p. Soil Sci. Soc. Am., Inc., Madison, WI, USA.

Kay, B. D., A. P. da Silva, and J. A. Baldock. 1997. Sensitivity of soil structure to changes in organic carbon contents: Predictions using pedotransfer functions. *Can. J. Soil Sci.* 77: 655-667.

Klute, A. 1986. Water retention: laboratory methods p. 635-662. In A. Klute (ed.) Methods of soil analysis. Part 1. 2nd ed. Agron. Monogr. 9. ASA and SSSA, Madison, WI.

Letey, J. 1985. Relationship between soil physical properties and crop production. *Advances in Soil Science.* B. A. Stewart, 277-94. Vol. 1. New York: Springer-Verlag.

Masle, J., and J. B. Passioura. 1987. The effect of soil strength on the growth of young wheat plants. *Aust. J. Plant Physiol.* 14: 643-56.

Peng S., K. G. Cassman, and M. J. Kropff. 1995. Relationship between leaf photosynthesis and nitrogen content of field-grown rice in tropics. Crop Sci. 35:1627-1630.

Rappoldt, C., and J. W. Crawford. 1999. The Distribution of Anoxic Volume in a Fractal Model of Soil. *Geoderma* 88: 329-47.

Rasiah, V., B. D. Kay, and E. Perfect. 1993. New Mass-Based Model for Estimating Fractal Dimensions of Soil Aggregates. Soil Sci. Soc. Am. J. 57: 891-95.

Renault, P., and J. Sierra. 1994. Modeling oxygen diffusion in aggregated soils: II. Anaerobiosis in top soil layers. Soil Sci. Soc. Am. J. 58:1023-30.

Schmidt, M.R., and M. R. Edwards. 1981. Photosynthesis capacity and nitrogen use efficiency of maize, wheat and rice: A comparison between C3 and C4 photosynthesis. J. of Exp. Bot. 32:459-466.

Sinclair, T. R., and T. Horrie. 1989. Leaf nitrogen, photosynthesis and crop radiation use efficiency: a review. Crop Sci. 9:451-454.

Tollenaar, M. and Migus, W. 1984. Dry matter accumulation of maize grown hydroponically under controlled-environment and field conditions. Can. J. Plant Sci. 64:475-485.

Tollenaar, M. 1989. Response of dry matter accumulation in maize to temperature. I. Dry matter partitioning. Crop Sci. 29: 1239-1246.

Tollenaar, M. 1999. Duration of the grain-filling period in maize is not affected by photoperiod and incident PPFD during the vegetative phase. Field Crops Res. 62: 15-21.

Van Keulen, H., J. Goudriaan., N. G., and N. G. Seligman. 1989. Modeling the effects of nitrogen on canopy development and crop growth, Plant Canopies: Their Growth, form and Function (G. Russell, B. Marshall, and P. G. Jarvis, eds.), Cambridge University Press. pp. 83-104.

von Caemmerer, S. and G. D. Farquhar. 1981. Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves. Planta 153:376-387.

Table 4.1. Selected characteristics of soils.

Soil #	Soil name	Clay	Silt	Sand	Textural class	O.C.	BDref	BD@ RC=0.83*	BD@ RC=0.91*	P	K	Mg	Ca	pH	Total N	C:N
		%	%	%		%	Mg m^{-3}	Mg m^{-3}	Mg m^{-3}	mg/kg	mg/kg	mg/kg	mg/kg		%	
1	Huron	40.6	48.2	11.2	Silty Clay	1.89	1.51	1.25	1.37	21	214	377	4292	7.8	0.129	14.7
2	Brookston	37.7	35.8	26.5	Clay Loam	1.80	1.52	1.26	1.38	24	206	443	3744	7.5	0.154	11.7
3	Huron	33.3	49.0	17.7	Silty Clay Loam	1.97	1.51	1.25	1.37	18	165	369	3960	7.7	0.133	14.8
4	Perth	27.2	48.5	24.3	Loam	1.50	1.54	1.28	1.40	13	126	417	3279	7.7	0.099	15.1
5	Conestogo	15.3	44.1	40.7	Loam	2.81	1.46	1.21	1.33	35	146	475	2152	6.5	0.161	17.5
6	Perth	13.7	22.6	63.7	Sandy Loam	3.74	1.39	1.15	1.26	14	148	301	3743	7.6	0.291	12.9
7	Fox	7.0	16.2	76.8	Sandy Loam	1.30	1.7	1.41	1.55	55	120	100	1459	6.9	0.064	20.3
8	Brady	5.5	30.1	64.4	Sandy Loam	2.62	1.43	1.19	1.30	11	63	206	4419	7.7	0.199	13.1

*OC, BD, and RC are organic carbon, bulk density and relative compaction respectively.

Table 4.2. Descriptive statistics of selected plant parameters (N=16)

Plant parameter	Mean	Minimum	Maximum	Standard deviation
Shoot wt (g)	35.1	24.2	47.8	7.12
Time to 12 leaf stage (days)	25.7	24.5	27.3	0.94
Rate of photosynthesis (μmoles m^{-2} sec^{-1})	19.4	16.5	21.4	1.51
Rate of whole plant transpiration (kg day^{-1})	0.32	0.23	0.43	0.06
Rate of leaf transpiration (mmoles m^{-2} sec^{-1})	2.57	2.06	3.18	0.32
Nitrogen uptake efficiency (kg kg^{-1})	0.358	0.138	0.527	0.122

Table 4.3. Regression equations relating plant parameters to soil properties.

Plant parameter	Regression equation*	R^2
Shoot wt (g)	$40.39 - 0.00777\ clay^2$	0.43
Time to 12 leaf stage (days)	$24.88 + 0.00125\ clay^2$	0.68
Rate of photosynthesis (μmoles m^{-2} sec^{-1})	$20.99 - 0.00230\ clay^2$	0.90
Rate of whole plant transpiration (kg day^{-1})	$0.360 - 0.000060\ clay^2$	0.36
Rate of leaf transpiration (mmoles m^{-2} sec^{-1})	$3.031 - 0.0206\ clay$	0.73
Nitrogen uptake efficiency (kg kg^{-1})	$0.470 - 0.000167\ clay^2$	0.71

*clay is the percent clay

Table 4.4 Concentrations of nutrients in shoot tissue.

Soil #	RC	N_c	N_t	P_c	P_t	K_c	K_t	Ca_c	Ca_t	Mg_c	Mg_t	Mn_c	Mn_t	Cu_c	Cu_t	Zn_c	Zn_t	B_c	B_t
		%	(g)	%	(g)	%	(g)	%	(g)	%	(g)	mg/kg	(mg)	mg/kg	(mg)	mg/kg	(mg)	mg/kg	(mg)
1	0.91	2.07	0.614	0.171	0.051	2.05	0.608	0.52	0.153	0.26	0.077	28	0.815	5	0.141	27	0.793	21	0.615
1	0.83	1.47	0.355	0.157	0.038	1.94	0.470	0.44	0.105	0.24	0.057	20	0.484	4	0.103	23	0.550	19	0.459
2	0.91	2.46	0.934	0.226	0.086	2.32	0.882	0.79	0.300	0.34	0.129	27	1.017	7	0.257	26	0.969	24	0.903
2	0.83	2.19	0.695	0.203	0.064	2.26	0.717	0.63	0.200	0.32	0.101	25	0.802	5	0.167	23	0.738	23	0.722
3	0.91	2.40	0.584	0.206	0.050	2.31	0.562	0.59	0.144	0.30	0.072	32	0.772	5	0.122	21	0.511	22	0.541
3	0.83	1.89	0.536	0.191	0.054	2.02	0.575	0.47	0.132	0.26	0.073	27	0.775	5	0.128	21	0.590	21	0.583
4	0.91	2.39	0.735	0.213	0.066	1.80	0.554	0.67	0.207	0.42	0.130	36	1.109	4	0.116	32	0.978	24	0.732
4	0.83	2.15	0.686	0.192	0.061	1.63	0.521	0.62	0.197	0.40	0.129	30	0.951	3	0.104	17	0.535	22	0.703
5	0.91	3.09	1.469	0.214	0.102	2.64	1.254	0.59	0.279	0.44	0.207	58	2.743	6	0.285	36	1.722	21	0.998
5	0.83	2.85	1.358	0.246	0.117	2.16	1.033	0.55	0.263	0.41	0.197	60	2.841	6	0.298	52	2.495	21	1.015
6	0.91	3.54	1.264	0.258	0.092	3.02	1.077	0.74	0.262	0.36	0.128	52	1.864	5	0.161	18	0.642	23	0.812
6	0.83	2.83	1.065	0.226	0.085	2.37	0.890	0.58	0.219	0.32	0.119	41	1.542	3	0.125	14	0.539	19	0.714
7	0.91	3.03	1.203	0.228	0.091	2.82	1.119	0.72	0.286	0.29	0.116	41	1.610	6	0.229	18	0.725	23	0.914
7	0.83	2.92	1.064	0.218	0.079	2.83	1.028	0.86	0.314	0.26	0.096	40	1.438	6	0.200	13	0.455	23	0.828
8	0.91	3.02	1.180	0.268	0.105	1.87	0.731	0.67	0.262	0.34	0.131	76	2.950	5	0.195	19	0.742	28	1.074
8	0.83	2.89	1.202	0.245	0.102	2.18	0.904	0.79	0.328	0.36	0.148	71	2.964	5	0.208	27	1.108	28	1.163

* Subscripts c and t refer to concentrations in shoot tissue and total amounts in shoot.

Figure 4.1. Variation in rate of photosynthesis with clay content

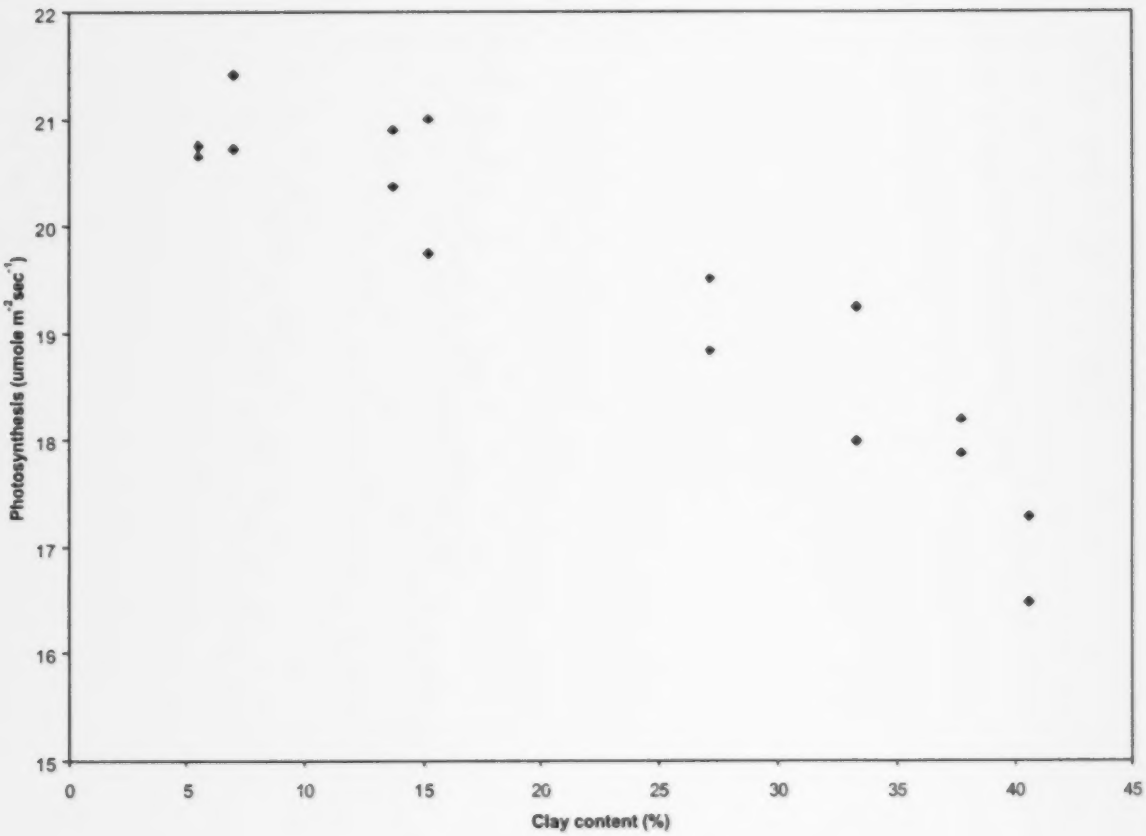


Figure 4.2. Variation in rate of photosynthesis with soil resistance to penetration

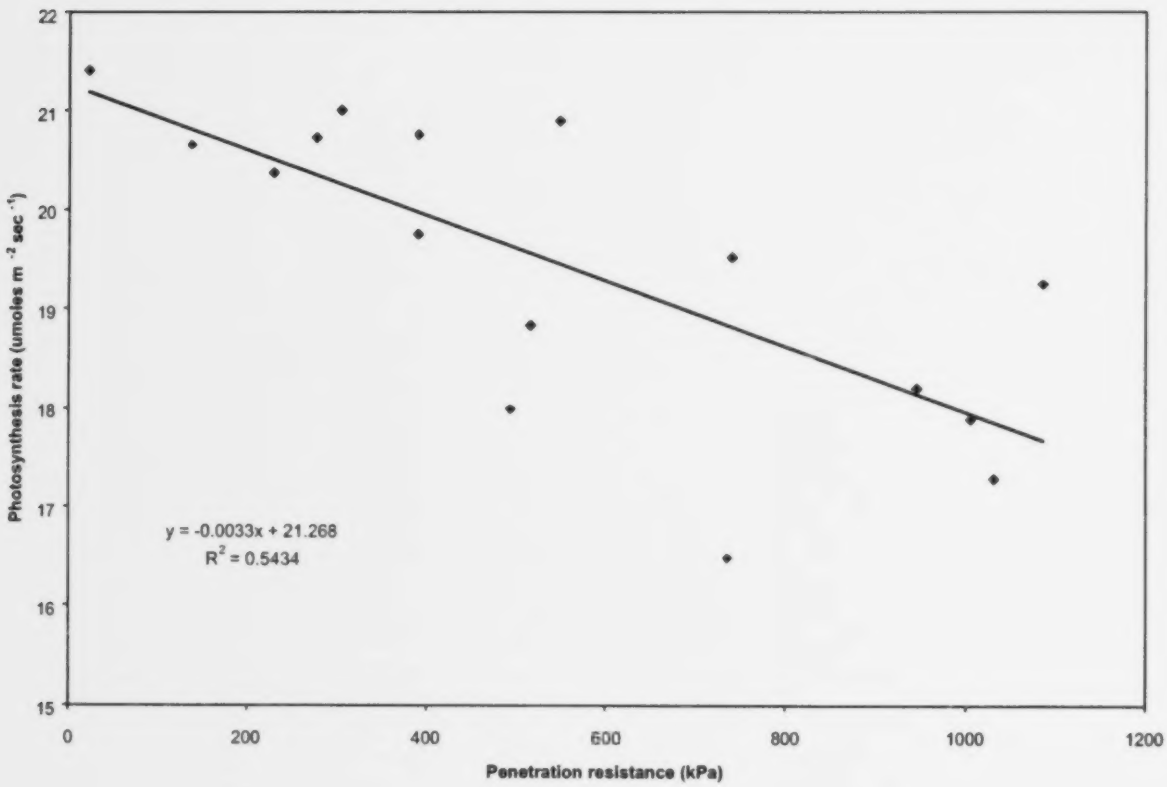


Figure 4.3. Variation in rate of photosynthesis with tissue N concentration.

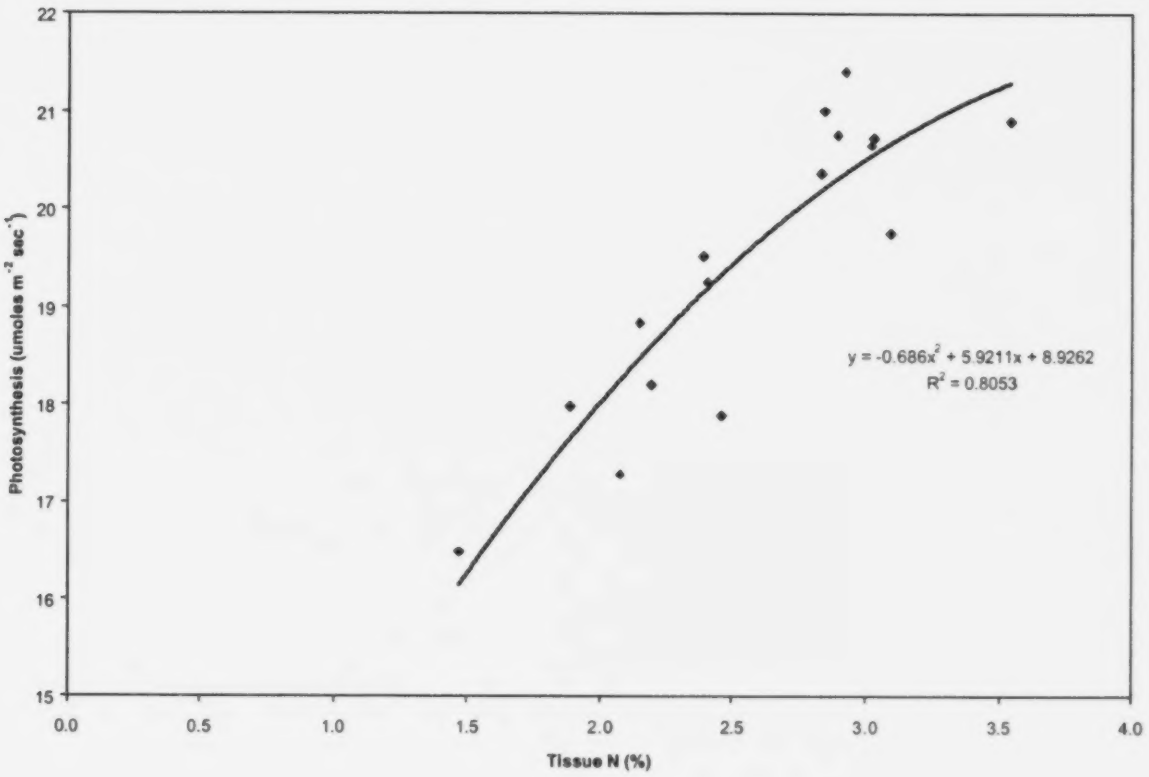


Figure 4.4. Variation in aggregate size with clay content.

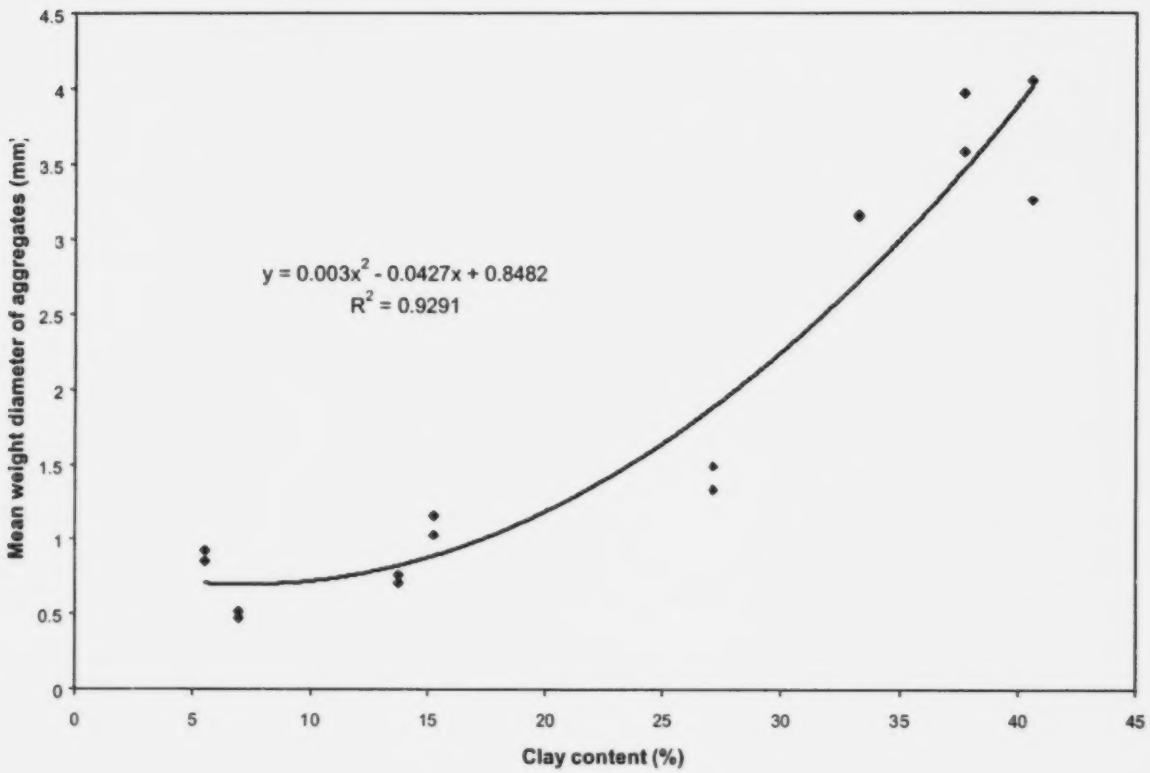


Figure 4.5. Variation in N and P content of shoot tissue with aggregate size.

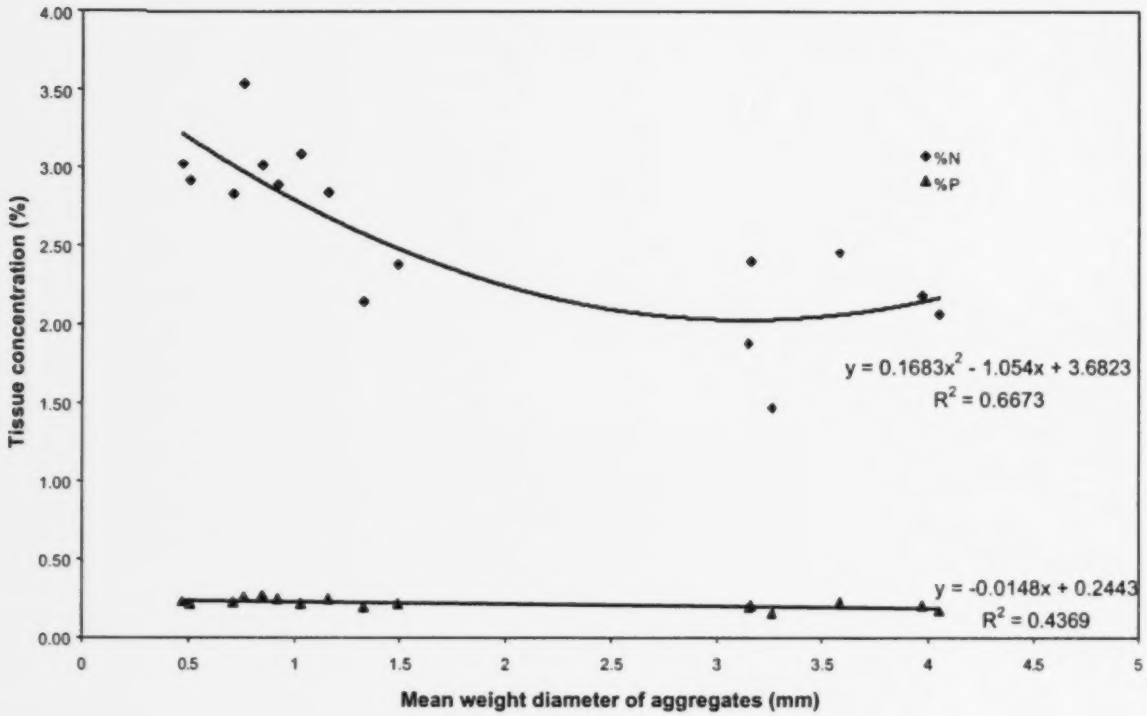
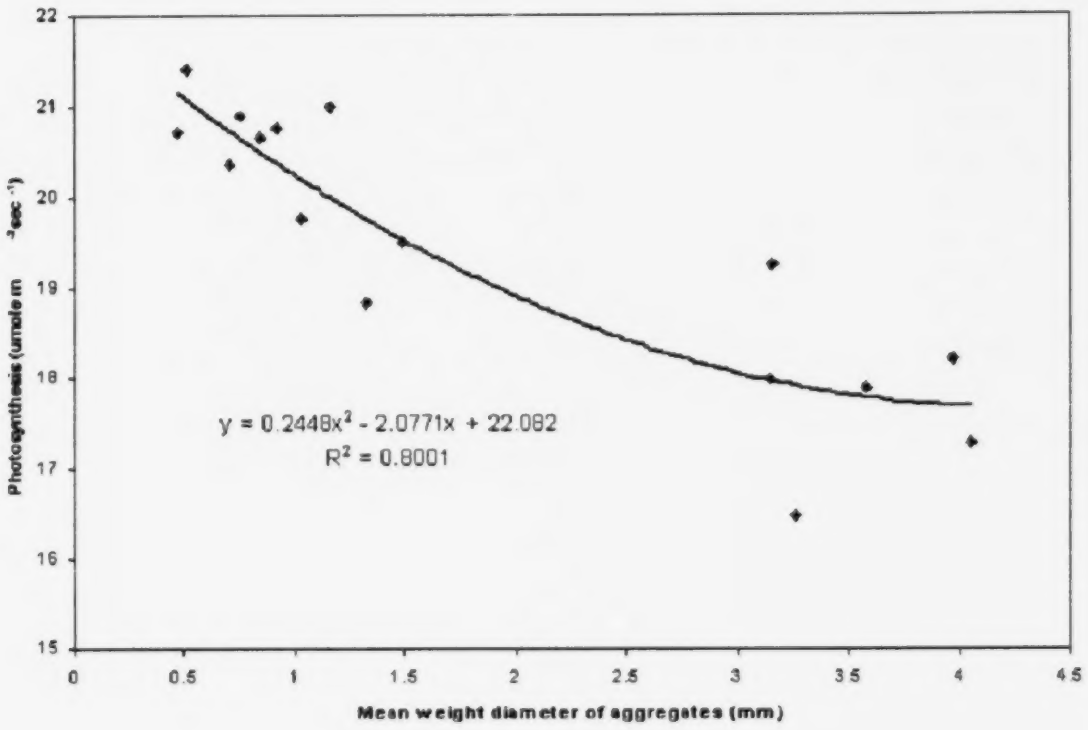


Figure 4.6. Variation in rate of photosynthesis with initial aggregate size distribution in pots.



5. Variation in transpiration and photosynthesis of maize during the dehydration of soils with different structure: identification of critical water contents.

5.1. Introduction

The functional dependence of transpiration and photosynthesis rates of different crops on the water content of soils, has been studied for purposes ranging from management of irrigation systems, to modeling crop growth or watershed hydrology. Although the nature of the function may vary with meteorological conditions, the shape of the function is often characterized using three critical water contents (θ). The upper critical limit (θ_{fdl}) corresponds to the water content remaining in the soil after rapid or free drainage has ceased. Aeration is assumed to not be limiting at this water content, and as the water content decreases to the second critical water content, the rates of transpiration and photosynthesis remain constant (these rates are sometimes referred to as the potential rates). The second limit approximates the threshold water content (θ_t), below which there is a rapid decline in the rates of transpiration and photosynthesis. The lower limit (θ_{ll}), corresponds to the water content at which the rates of transpiration and photosynthesis approach zero or some arbitrary fraction of the potential rate. The three critical values can be used to derive four additional important parameters. The difference between θ_{fdl} and θ_t describes a range in water content that is non-limiting to gas exchange. The difference between the upper and the lower limit is referred to as the total transpirable water (TTW). The amount of water potentially available for transpiration at any time, expressed as a fraction of the total transpirable water (PAW) is $(\theta-\theta_{ll})/(\theta_{fdl}-\theta_{ll})$. The fraction of the TTW remaining in the soil at θ_t (PAW_t) is defined by $(\theta_t-\theta_{ll})/(\theta_{fdl}-\theta_{ll})$. Sadras and Milroy (1996), in a comprehensive review of threshold water contents for leaf expansion and gas exchange, noted that PAW_t varied with species and genotypes, evaporative demand, and was generally higher for expansion of plant tissue than for gas exchange. They also noted inconsistent conclusions related to the effect of soil properties on PAW_t and concluded that the influence of soil properties on PAW_t merited further research.

Variation in the rates of transpiration and photosynthesis of maize during soil drying (under a given evaporative demand), would be expected to reflect the integration of decreasing soil water content on declining water potential, improved aeration and increasing resistance to penetration encountered by growing roots. Consequently, the critical water contents could be used as characteristics of the structure of soil.

The role of a combination of water potential, aeration and soil resistance in defining the critical water contents, particularly θ_t and θ_{ll} has received little attention. Variation in soil structure arising from differences in texture, organic carbon (OC) content and the extent of soil of compaction are known to influence the dependence of water potential, aeration and soil

resistance on water content (Kay et al. 1997). However, the lack of understanding of the combined effects, particularly of potential and soil resistance, on the critical water contents means that impact of variation in texture, OC and soil compaction on the critical water contents cannot be predicted.

5.2. Objectives

The objectives of this study were to: (a) determine the influence of soil texture, OC content, and the extent of soil compaction on θ_{fdl}-θ_t, θ_{fdl}-θ_{ll} and $(\theta_t$-$\theta_{ll})/(\theta_{fdl}$-$\theta_{ll})$ for transpiration and photosynthesis of young maize plants grown in controlled environment rooms, and (b) identify the role of water potential, aeration and soil resistance to penetration in defining these critical ranges in water content.

5.3. Materials and methods

Details on the soils used in this study, their packing and preparation for planting, and the conditions for growing the plants to the 12 leaf stage, are given in the preceding chapter. The experimental design involved 8 soils, 2 levels of relative compaction, 2 watering treatments and 4 replications.

Up to the 12-leaf stage (the 12th leaf was visible in the whorl) all of the plants were regularly watered to return the soil water contents to that corresponding to an air-filled porosity (volume air/volume total soil) of 0.10. The watering treatments, which consisted of a drying treatment (water withheld) and a control (rewatering to an air-filled porosity of 0.10), were introduced at the 12 leaf stage. In order to minimize plant to plant shading, the pots in each replicate were rearranged with the plants in the drying treatment (16) put in one growth cabinet and those in the control (16) placed in another growth cabinet. The pots from both the drying and control treatments were completely enclosed in white plastic bags and the bags tightened around the base of the stem to prevent soil evaporation. The pots were weighed at the end of each light period every night between 20:00 and 21:00 p.m. and water added to control. This timing maximized the opportunity for water redistribution in the pots prior to the start of the next light period. Average daily volumetric soil water contents and daily transpiration on a whole plant basis were calculated from the weights of the pots after adding water and at the end of the light period. The rates of transpiration and photosynthesis were measured daily on a unit leaf area basis following the procedures outlined in chapter 4.

The drying treatment was terminated when the photosynthesis and leaf transpiration rates decreased to about 10% of the control. Above-ground plant material (shoot) was harvested for all the treatments and roots were carefully washed from soils for three replicates of the drying

treatments. Both shoot and root were dried at 80°C to constant weight. Nutrient contents of the shoot biomass were determined for both watering treatments.

5.4. Results and discussion

Transpiration and photosynthesis varied with soil water content during the drying period in the expected manner (data for rates of photosynthesis, at 27% clay, relative compaction = 0.83, rep 1 is provided in Fig. 5.1 to illustrate the relation). Different functions (quadratic, first order exponential growth, logistic, Gompertz and piecewise linear) to describe the relation between the gas exchange parameters and soil water content plant were compared by applying nonlinear estimation techniques (Statsoft 1999) to a representative set of the data. The comparison indicated that the logistic and piecewise linear regressions gave higher R^2 than the other functions. The logistic and piecewise linear functions were then applied to the daily whole plant transpiration (T_p) data for the average of the 4 reps for each of the 16 soils in order to select the most appropriate function. The logistic function was of the form:

$$T_p = T_{p\,pot} /(1 + \exp a(\theta\text{-}b)) \qquad (5.1)$$

where $T_{p\,pot}$, a and b are constants in the regression equation with $T_{p\,pot}$ representing the maximum transpiration rate (potential transpiration). Values of θ_t and θ_{ll} were calculated from Eqn 1 setting $T_p/T_{p\,pot}$ to 0.95 and 0.10, respectively. The piecewise linear function was of the form:

$$T_p = (a + b\theta) \text{ when } \theta \leq \theta_t \text{ and } (a+b\theta_t) \text{ when } \theta > \theta_t. \qquad (5.2)$$

where θ_t, a and b are constants in the regression equation. $T_{p\,pot}$ is equal to $(a + b\theta_t)$. Values of θ_{ll} were calculated setting $T_p/T_{p\,pot}$ to 0.10 and 0.00. Values of R^2 were similar for the two functions (R^2 varied from 0.895 to 0.998 for the logistic function and from 0.915 to 0.999 for the piecewise linear estimation). Values of θ_t calculated from the logistic function were equal to or slightly greater than those calculated from piecewise linear fit. However, larger differences were noted for θ_{ll} estimated from the two equations. The exponential approach to minimum values of the dependent variable in the logistic function, characteristic of S-shaped functions, resulted in values of θ_{ll} calculated at $T_p/T_{p\,pot} = 0.10$ always being smaller than those calculated from the piecewise linear equation. This characteristics of the logistic function also prevented a value of θ_{ll} being calculated at $T_p/T_{p\,pot} = 0.00$. Consequently, the piecewise linear analysis was applied to all of the gas exchange data to estimate values of θ_t and θ_{ll}. The use of this function is illustrated in Fig. 5.1. Values of θ_{ll} were calculated at $T_p/T_{p\,pot} = 0.00$.

The accuracy of estimates provided by the piecewise linear analysis procedure were assessed by comparing the calculated values of the maximum or potential rate of whole plant

transpiration ($T_{p\ pot}$), leaf transpiration ($T_{l\ pot}$), and photosynthesis ($P_{l\ pot}$), with the corresponding parameters that were observed for the control treatment. Since the studies were carried out in a controlled environment, values of the calculated maximum rates of gas exchange in the drying treatment should be equal to the rates of exchange of the control during the period that the water contents of the drying treatment were decreasing from the value of the control to θ_t, if the estimates from the curve-fitting procedure are accurate. No statistically significant differences between the estimated values and the observed values were found for measurements based on either of the three gas exchange parameters (the correlation between the observed values and calculated values for the rates of photosynthesis is illustrated in Fig. 5.2), illustrating the accuracy of the curve-fitting procedure.

Values of θ_{fdl}, and of θ_t and θ_{ll} obtained from measurements of the different gas exchange parameters are given in Table 5.1. Small, but significant, differences existed in values of θ_t and θ_{ll} derived from the different measurements. However, the differences were not consistent. The mean θ_t derived from leaf transpiration measurements was 0.02 $m^3\ m^{-3}$ larger than the values derived from either the whole plant transpiration or photosynthesis measurements. The mean of θ_{ll} derived from leaf transpiration and photosynthesis were 0.02 $m^3\ m^{-3}$ larger than corresponding values for whole plant transpiration. The differences in θ_t and θ_{ll} due to measurement were also not consistent between soils. Consequently, there was no evidence that estimation of the critical water contents varied in a systematic manner with the different gas exchange parameters.

A correlation matrix of the critical water content variables showed that θ_{fdl} was not correlated with values of θ_t or θ_{ll} derived from any of the gas exchange measurements. However, θ_t was correlated with θ_{ll} with correlation coefficients varying from +0.82 for whole plant transpiration to +0.94 for photosynthesis.

Values of θ_{fdl}-θ_t, θ_{fdl}-θ_{ll}, and (θ_{fdl}-θ_t)/ θ_{fdl}-θ_{ll}) were calculated, and then related to soil properties (clay, silt, sand and OC contents and their squared terms, and relative compaction) using simple linear simple regression. Variables exhibiting significant correlations were then used in forward stepwise multiple regression (Statsoft 1999) to identify the combination of soil characteristics most strongly correlated with these water parameters. The resulting regression equations are given in Table 5.2. Values of both θ_{fdl}-θ_t and θ_{fdl}-θ_{ll} increased with decreasing clay content and increasing OC content (the exception being θ_{fdl}-θ_t derived from whole plant transpiration measurements where the OC term was significant at P=0.053). Values of (θ_{fdl}-θ_t)/θ_{fdl}-θ_{ll}) were either not correlated with soil properties (values derived from leaf transpiration and photosynthesis) or were very weakly correlated (pot transpiration). The average values of (θ_{fdl}-θ_t)/θ_{fdl}-θ_{ll}) were 0.32, 0.35 and 0.30 for values derived from whole plant transpiration, leaf transpiration and photosynthesis, respectively. These values compare favorably with the values

tabulated by Sadras and Milroy (1996), which were derived under similar conditions. However, they do not provide convincing evidence of the variation with texture, which Sadras and Milroy speculated may have existed when they reviewed data collected by different investigators working on different soils using different techniques. Relative compaction was not a significant covariate for any of the water content parameters and this may indicate that the range in relative compaction was not large enough to create significant effects.

Data on the variation with water content of water potential and soil resistance to penetration were used to assess the role of these factors in limiting gas exchange at θ_t. Values of water potential at θ_t, derived from photosynthesis measurements, varied from -0.01 to -0.15 MPa with a mean of -0.06 MPa. Values of soil resistance to penetration at corresponding values of θ_t varied from 0.48 to 3.70 MPa with a mean value of 1.70 MPa. However, the relation between soil resistance and water potential was remarkably different for soils with clay contents ≥27% compared to those of soils with clay contents ≤15% (Fig. 5.3). Values of soil resistance increased with decreasing water potential for soils with clay contents ≥27% but exhibited little variation with potential for soils with clay contents ≤15% (Fig. 5.3). Values of water potential and soil resistance to penetration at θ_t derived from leaf and whole plant transpiration exhibited similar trends (mean values of water potential were 0.05 and 0.06 MPa, respectively and mean values of soil resistance were 1.48 and 1.67 MPa respectively). A variation in water potential and in soil resistance to penetration at θ_t of the magnitude illustrated in Fig 5.3 suggests that the water content at θ_t cannot be defined on the basis of a single limiting value of either water potential or soil resistance to penetration. We speculate that the water content at which water potential begins to decrease rapidly and/or the soil resistance begins to increase rapidly may be a more important than a given value of potential or soil resistance.

Although a critical water content at which soil resistance begins to increase rapidly could not be identified for soils with clay contents ≤15% (since the soil resistance of these soils varied quadratically with water content, declining to low soil resistance at low water contents) the following procedure was used with the remaining soils. The changes in soil resistance to penetration with change in water content were calculated and plotted against water content, the data fitted to two intersecting straight lines using piecewise linear estimation techniques (Statsoft 1999) and the water content at the point of intersection (θ_{srb}) identified. The water content at 0.001 MPa (equivalent to half the height of the soil column in the pots and therefore the average water potential in the pots when free drainage had ceased) ($\theta_{0.001MPa}$) was obtained from the water release data, and values of ($\theta_{0.001MPa}$-θ_b) calculated. These values were then correlated to values of (θ_{fdl}-θ_t):

$$(\theta_{0.001MPa}-\theta_{srb}) = -0.0314 +1.092\ (\theta_{fdl}-\theta_t)\ R^2 = 0.91 \qquad 5.3$$

A similar approach was applied to the water release curve. The water content was identified at which the change in water potential with water content began to increase rapidly in magnitude, i.e., θ_{wpb}. Not surprisingly, these values were correlated to the breakpoint on the soil resistance curve:

$$(\theta_{0.001MPa}-\theta_{srb}) = -0.1355 + (\theta_{0.001MPa}-\theta_{wpb})\ R^2 = 0.97 \qquad 5.4$$

These analyses suggest that, at least for soils with clay contents ≥27%, gas exchange rates began to decline from the maximum values at θ_t when the soil resistance and/or water potential began to change rapidly with small decreases in water content and that the rates of change with water content were more important than the magnitude of either the potential or soil resistance. The factor(s) responsible for the rapid decline in gas exchange in soils with clay contents ≤15% may be similar to those in soils with higher clay contents. When values of $(\theta_{0.001MPa}-\theta_{wpb})$ were used for for soils with clay contents ≤15% and the larger of either $(\theta_{0.001MPa}-\theta_{wpb})$ or $(\theta_{0.001MPa}-\theta_{srb})$ i.e., $(\theta_{0.001MPa}-\theta_{wp\ sr\ b})$, were used for soils with clay contents ≥27%, the following correlation was obtained:

$$(\theta_{fdl}-\theta_t) = 0.080 + 0.62(\theta_{0.001MPa}-\theta_{wp\ srb})\ R^2 = 0.59 \qquad 5.5$$

This relation is superior to using either $(\theta_{0.001MPa}-\theta_{wpb})$ or $(\theta_{0.001MPa}-\theta_{srb})$ on their own. The analyses suggest that $(\theta_{fdl}-\theta_t)$ can be predicted from the water release curve and the soil resistance curve. However, it should be noted that greater variability in $(\theta_{fdl}-\theta_t)$ can accounted for using texture and OC data (Table 5.2) than the water release and soil resistance data (0.74 as compared to 0.59).

Data on the variation with water content of water potential and soil resistance to penetration were also used to assess the role of these factors in limiting gas exchange at θ_{ll}. Values of water potential varied from -0.31 to -1.5 MPa at θ_{ll}, whereas soil resistance varied from 0.1 to 11.8. The soils with lower clay contents had the lowest water potentials and the smallest soil resistances. For instance, the soil with 5% clay had limiting values of water potential of -1.5 MPa at both levels of relative compaction and soil resistances of 0.82 and 0.10 MPa and a relative compaction of 0.91 and 0.83 respectively. The data suggest that water potential was the limiting factor on the coarse-textured soils. The finest textured soils (clay contents ranging from 33-41%) had an average water potential of -0.56 MPa at θ_{ll} and an average soil resistance of 7.0 MPa, indicating soil resistance was the limiting factor. While these trends are compatible with predictions using pedotransfer functions (Kay et al. 1997), the limiting value of soil resistance was much higher than that assumed in calculations of a least limiting water range (e,g., a limit of 2.0 MPa assumed by da Silva et al (1997)). The limiting factor in soils with intermediate textures (7-27 % clay) was more difficult to identify with water potentials and soil resistance falling between the above limits. However, if the limiting conditions are assumed to

be the larger water content of either a potential of -1.5 MPa or a soil resistance of 7 MPa ($\theta_{wp\ sr}$), values of ($\theta_{0.001MP}$-$\theta_{wp\ sr}$) can be correlated with (θ_{FDL}-θ_{ll}) and give:

$$(\theta_{FDL}-\theta_{ll}) = 0.05 + 0.83(\theta_{0.001MP}-\theta_{wp\ sr}) \quad R^2=0.75 \qquad 5.6$$

The intercept was not significantly different from zero. When available water was used as the independent variable ($\theta_{0.001MP}$-$\theta_{0.15MPa}$), the R^2 and the slope improved slightly:

$$(\theta_{FDL}-\theta_{ll}) = 0.01 + 1.0(\theta_{0.001MP}-\theta_{wp\ sr}) \quad R^2=0.79 \qquad 5.7$$

The intercept was not significant. The strong relation with available water suggests that, although soil resistance may be the limiting factor at θ_{ll} in soils with the highest clay content, the shape of the water release curve in this range of water contents is such (small changes in water content over large changes in potential) that errors in taking the water content at a water potential of -1.5 MPa as the limiting water content are small.

Once again, a larger part of the variability in (θ_{FDL}-θ_{ll}) was accounted for when texture and organic carbon were used as predictors than when a combination of soil resistance and water potential characteristics were used (0.93 versus 0.75 or 0.79, respectively).

5.5. Conclusions

Texture and OC content had a strong influence on both (θ_{FDL}-θ_t) and (θ_{FDL}-θ_{ll}) with more of the variability in (θ_{FDL}-θ_{ll}) accounted for by these variables than was the case for (θ_{FDL}-θ_t). The size of both ranges increased with OC content and decreased with clay content. PAW_t was not strongly correlated with soil characteristics and had an average value (across soils, levels of relative compaction and gas exchange characteristics) of 0.32. Values of (θ_{FDL}-θ_t) did not appear to be related to a critical value of either water potential or soil resistance, but θ_t did appear to be related to water contents in which either water potential began to decrease rapidly with decreasing water content and/or soil resistance began to increase rapidly with decreasing water content. Values of (θ_{FDL}-θ_{ll}) appeared to be controlled by a limiting soil resistance in fine textured soils and by water potential in coarse textured soils. Although these trends were expected, it was surprising to find that the limiting soil resistance at θ_{ll} appeared to be about 7 MPa rather than 2 MPa as is customarily assumed. Values of (θ_{FDL}-θ_{ll}) could be predicted equally well from only available water, presumably because the shapes of both the water release curves and the soil resistance curves for the fine textured soils show small variation in water content across large changes in either water potential or soil resistance at these water contents.

5.6. Literature cited

da Silva, A. P., and B. D. Kay. 1997. Estimating the least limiting water range of soils from properties and management. *Soil Sci. Soc. Am. J.* 61: 877-83.

Kay, B. D., A. P. da Silva, and J. A. Baldock. 1997. Sensitivity of soil structure to changes in organic carbon contents: Predictions using pedotransfer functions. *Can. J. Soil Sci*. 77: 655-667.

Sadras, V. O., and S. P. Milroy. 1996. Soil-water thresholds for the responses of leaf expansion and gas exchange: A review. *Field Crops Res.* 47: 253-66.

Statsoft 1999. Statistica for Windows. Statsoft Inc. Tulsa, OK, USA.

Table 5.1 Values of the water content at the free drainage limit and critical water contents derived from different gas exchange measurements.

Clay content %	R C	θ_{fdl}	Whole plant transpiration		Leaf transpiration		Photosynthesis	
			θ_t	θ_{II}	θ_t	θ_{II}	θ_t	θ_{II}
40.6	0.91	0.45	0.259	0.15	0.278	0.187	0.273	0.187
40.6	0.83	0.42	0.281	0.125	0.258	0.167	0.260	0.166
37.7	0.91	0.45	0.240	0.164	0.274	0.174	0.266	0.182
37.7	0.83	0.43	0.234	0.154	0.280	0.159	0.240	0.163
33.3	0.91	0.45	0.258	0.139	0.264	0.168	0.252	0.170
33.3	0.83	0.41	0.208	0.123	0.276	0.138	0.256	0.146
27.2	0.91	0.40	0.219	0.085	0.197	0.116	0.180	0.118
27.2	0.83	0.40	0.194	0.090	0.204	0.103	0.188	0.107
15.3	0.91	0.49	0.209	0.070	0.184	0.081	0.187	0.081
15.3	0.83	0.52	0.195	0.085	0.199	0.093	0.189	0.093
13.7	0.91	0.50	0.221	0.073	0.252	0.107	0.233	0.105
13.7	0.83	0.50	0.180	0.076	0.225	0.086	0.184	0.090
7.0	0.91	0.35	0.107	0.046	0.165	0.044	0.154	0.046
7.0	0.83	0.35	0.131	0.030	0.160	0.044	0.148	0.044
5.5	0.91	0.44	0.141	0.058	0.194	0.068	0.170	0.073
5.5	0.83	0.42	0.181	0.043	0.144	0.065	0.146	0.067
Mean		0.435	0.204	0.095	0.222	0.112	0.208	0.115

Table 5.2 Regression equations relating critical water contents to soil properties for different gas exchange measurements.

Dependent variable	Gas exchange parameter	Regression equation*	R^2
θ_{fdl}-θ_t	Whole plant transpiration	0.264 - 0.000056 Cl^2	0.49
	Leaf transpiration	-0.0044 + 0.195 OC - 0.033 OC^2 - 0.000055 Cl^2	0.74
	Photosynthesis	0.169 + 0.397 OC - 0.000044 Cl^2	0.74
θ_{fdl}-θ_{ll} (TTW)	Whole plant transpiration	0.248 + 0.053 OC - 0.000037 Cl^2	0.88
	Leaf transpiration	0.255 + 0.046 OC - 0.000050 Cl	0.87
	Photosynthesis	0.129 +0.168 OC - 0.000064 Cl^2 - 0.0246 OC^2	0.93
$(\theta_{fdl}-\theta_t)/(\theta_{fdl}-\theta_{ll})$ (PAW_t)	Whole plant transpiration	0.243 + 000051 Si^2	0.25
	Leaf transpiration	-	-
	Photosynthesis	-	-

* Cl, Si and OC are the clay, silt and organic carbon contents (%), respectively.

Figure 5.1 Illustration of relation of whole plant transpiration to soil water content (27 % clay, relative compaction = 0.83, rep1) using piecewise linear regression. For this specific sample, θt is 0.24 m^3 m^{-3}

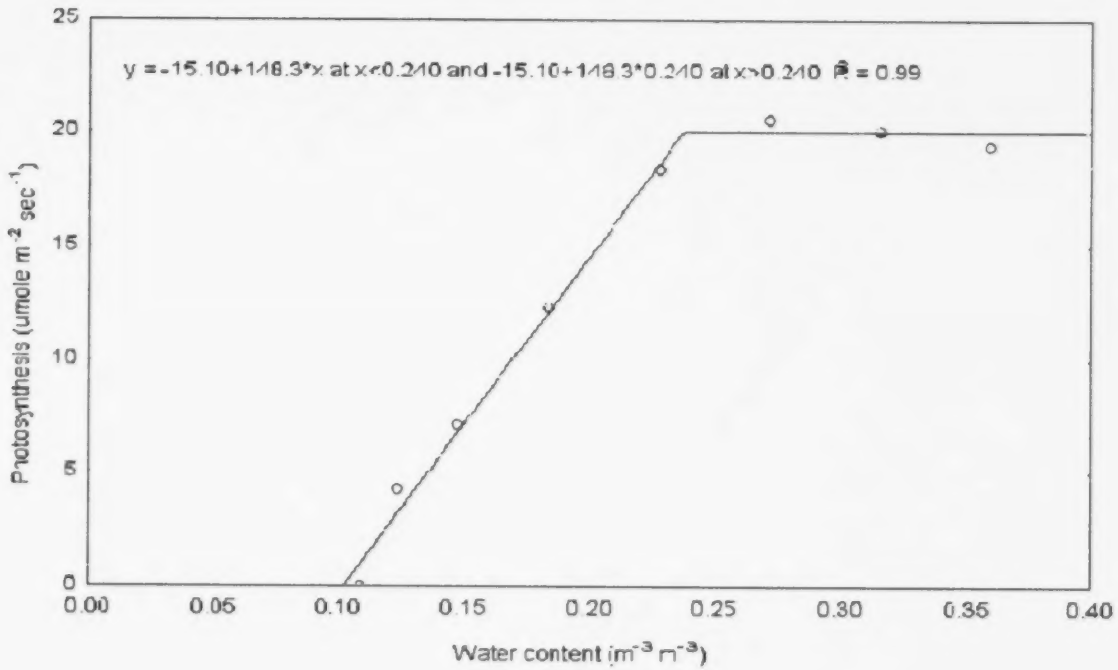


Figure 5.2 Comparison of maximum rate of photosynthesis in the drying treatment (calculated from eqn. 5.2) with average rate of photosynthesis observed in the control treatment over the same time.

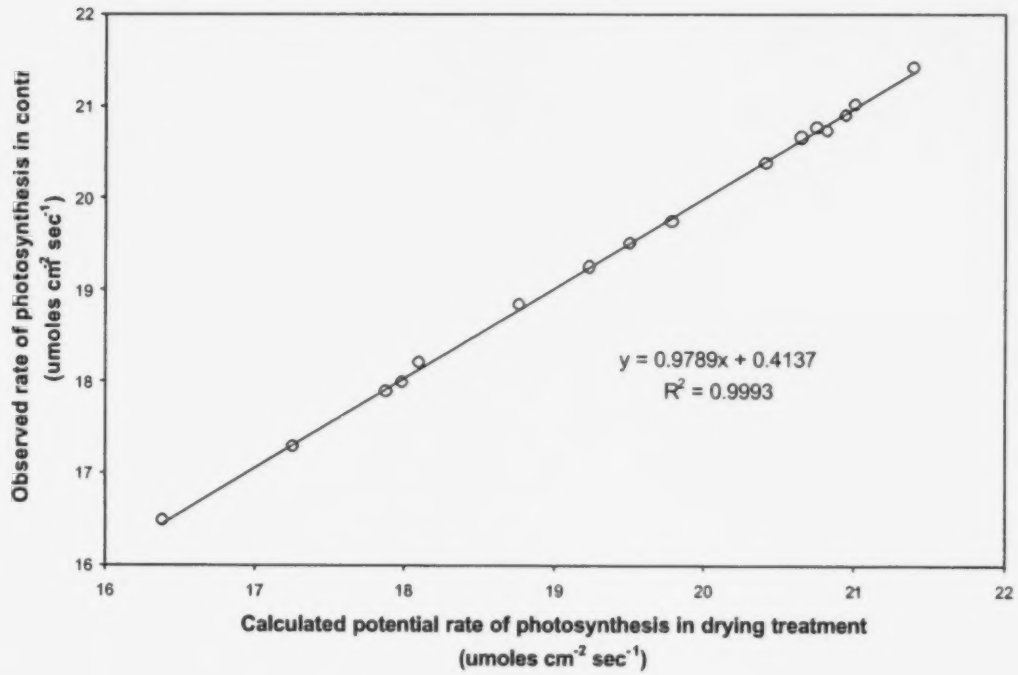
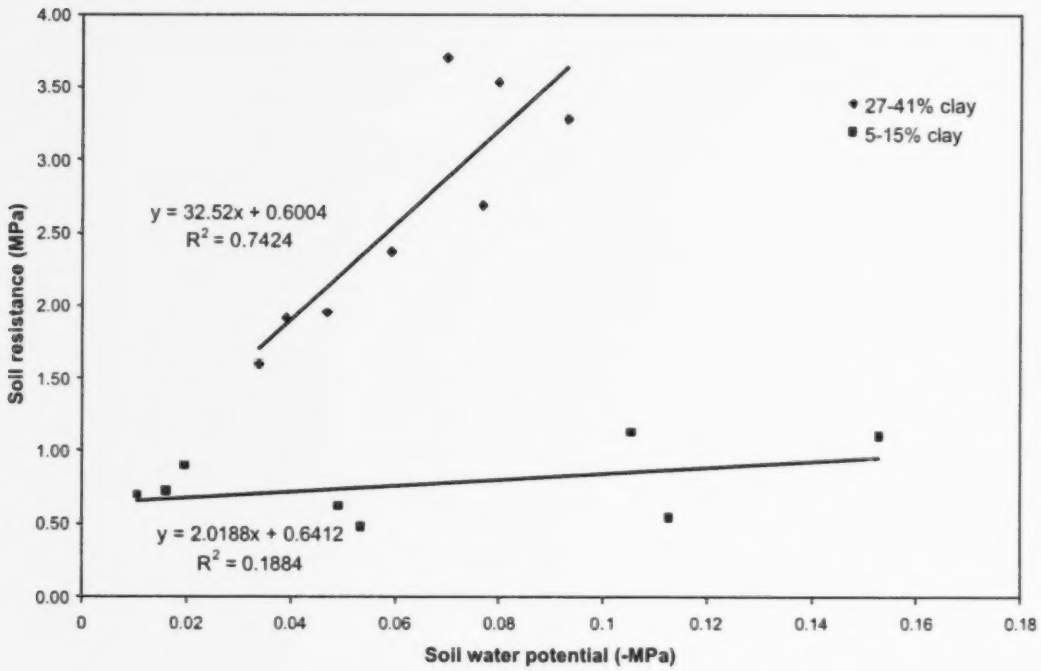


Figure 5.3 Variation in soil resistance with water potential at θ_t derived from measurements of rates of photosynthesis.



6. Variation in transpiration and photosynthesis with soil water regime: influence of hybrid and stage of development.

6.1. Introduction

The variation in gas exchange characteristics with soil water regime in controlled environments is commonly studied using a single stage of development (normally seedling or early vegetative stage) and water contents that are well below the free drainage limits of pots (conditions under which aeration would seldom be limiting). The possibility has been considered by few researchers that transpiration and photosynthesis may vary with decreasing water potential, increasing soil resistance to root penetration or increasing aeration (acting singly or in combination) and that the variation may be a function of hybrid or stage of development. The role of hybrids on critical water contents (chapter 4) has been examined by Ray and Sinclair (1997) when plants with three to four fully expanded leaves growing under greenhouse conditions were stressed by drying. Their measurements of transpiration on eight hybrids suggested that estimates of the total transpirable water (θ_{fdl}-θ_{ll}) of the soil - bark mixture, which was used as the potting medium, did not vary with hybrid. However, estimates of the fraction of transpirable water remaining in the medium when normalized transpiration began to decline, (θ_t-θ_{ll})/(θ_{fdl}-θ_{ll}), exhibited significant differences among hybrids. Corresponding studies have not been conducted at different stages of development.

The impact of increasing water content towards saturation (with resulting decreasing air-filled porosity and oxygen supply) on gas exchange may vary with hybrid and stage of development, but may also vary with soil structure and with the duration of high water contents. Lipiec et al. (1996) found that a reduction in the air-filled pore space to less than 0.10 during the period 9-22 days after emergence, did not result in any increase in stomatal resistance of maize when the bulk density was 1.28 Mg m^{-3}. However, at a bulk density of 1.58 Mg m^{-3}, the stomatal resistance began to increase as the air-filled porosity decreased below values as high as 0.25. Studies on the response of a single maize hybrid to saturation of the root zone under field conditions (Lizaso and Ritchie 1997) have shown that plant responses were similar when saturation occurred at the five to six and ten to twelve leaf tip stages. The magnitude of the response increased, however, as the duration of the saturation period increased from four to eight days. There is no information on possible variation between maize hybrids in these cases.

6.2. Objectives

The objective of this study was to determine if the variation in transpiration and photosynthesis with water contents, ranging from saturation to a lower limit of transpirable water, were influenced by hybrid and stage of development.

6.3. Materials and methods

Conestogo silt loam and Fox sandy loam (soils # 5 and 7, Table 4.1) were employed in this study. The soils were air-dried on plastic sheets in greenhouse bench, sieved (<6 mm) and analyses of texture, OC content, and selected chemical properties completed (Table 4.1). Plastic pots with a volume of 1.5- , 6- and 22-L were used for experiments at the 6-leaf stage, 15-leaf stage, silking, and grain filling period. Nutrients, in the form of dry reagent grade chemicals (NH_4NO_3, $Ca(H_2PO_4)_2*2H_2O$, and K_2SO_4) were weighed out for each pot and then added to the soil at rates of 100 ppm P, 50 ppm K, and 200 kg N ha^{-1} (P and K were added on a unit soil weight basis recognizing that these nutrients are more reactive with the soil than N and the pots contain different weights of soil). Four to 10 additional drainage holes were drilled at the base of the side of the pots. The soil was then packed in plastic pots to a bulk density 1.33 (relative compaction = 0.91) for the Conestogo soil and 1.4 g cm^{-3} (relative compaction =- 0.83) for the Fox soil. Soil was packed in the pots in 3 cm depth increments for the 1.5- ,6 L pots and 10-cm increments for the 22-L pots. Pots were then wet from the base to saturation with distilled water and submerged for 1-3 days (depending on texture). The pots were then removed from the containers in which they were saturated, covered with plastic to prevent evaporation, and allowed to drain until there was no further water loss. The equilibrium water content (normally achieved within 2 days) was referred to as the free drainage limit (fdl). Additional pots that were packed at the same time, saturated and drained in a similar manner were used to assess the uniformity in packing. No statistically significant variation in bulk density was found on sampling radially or with depth in the pots. Supplementary pots were also prepared to characterize soil structure and determine the water release curve.

Two maize hybrids, Pride 5 and Pioneer 3902 were used in this series of experiments. Pride 5 (double-cross hybrid) was introduced in 1959 and was one of the first maize hybrids to be widely gown in Central Ontario. Pioneer 3902 (single-cross hybrid) was introduced in 1988 and was one of the most widely grown hybrids in Central Ontario during the 10 years after its initial release. These two hybrids have similar morphology, phenology, and relative maturity but differ greatly under water-deficit stress condition (Tollenaar 1989, Nissanka et al. 1997). Seeds were placed in a solution of 50% of bleach and 50% of water, stirred for 15 min to sterilize, rinsed thoroughly with deionized water, and then soaked in an aerated water 48 hr for pre-germination. Prior to sowing, seeds were immersed in 2% Benelate, a wettable fungicide powder containing 50% of Benomyl (Dupont Canada Inc.) for 20 min. Three pre-geminated

seeds were planted to each pot and seedlings were thinned to one plant at the 3-leaf stage. A layer of sand about 1 cm in depth was used to cover the pot surface to prevent soil evaporation. The number of visible leaf tips was recorded every day in the growth cabinets. Plants within a growth cabinet and growth room were periodically rotated to minimize plant-to-plant variability. The experiment was laid out as a randomized complete block design with two hybrids, four stages of development, two soils (one soil only for experiments during silking and grain-filling period), three wetting treatments (a control, a drying and a saturation treatment) and four replications. Because of the size, the experiment was arranged on the basis of stage of development.

Once the plants reached the 6 (the 6th leaf was visible in the whorl), 12 leaf, and silking and grain filling stages, the drying and water logging treatments were imposed. The drying treatment involved completely enclosing the pots in white plastic bags that were subsequently tightened around the base of the stem to prevent soil evaporation and then allowing the pots to dry until gas exchange rates fell to about 10% of the maximum rates. The pots were weighted every night between 20:00 and 21:00 (EST) to determine transpiration on a pot basis. The waterlogging treatment involved placing the pots in plastic containers that were taller than the pots and increasing the water level in the containers until the water level in the pots was about 2cm above the level of the sand at the top of the pots. The water level was maintained until the drying treatment was terminated. The control treatment involved encasing the pots in plastic, as in the drying treatment. The pots were weighed at the same time as the drying treatment and water added to return the water content to that equivalent to 10% air-filled porosity. The timing of the water addition maximized the opportunity for water redistribution in the pots prior to the start of the next light period.

The experiments were conducted in controlled-environment growth cabinets (Model PGW36, Controlled Environments, Winnipeg, Manitoba). Growth conditions were 26/16 °C day/night temperature, with a 16-h photoperiod, and a relative humidity of approximately 75%. The PPFD was maintained at approximately 650 μmol m^{-2} s^{-1} at the top of the canopy, with a mixture of 'cool white' fluorescent tubes and 'inside frost' tungsten bulbs (Osram Sylvania, Drummondville, Quebec). Air temperature in each growth cabinet was continuously monitored with thermocouples positioned closely to the whorls of four plants. For experiments at the 15-leaf stage , silking and the grain-filling period, plants were grown in controlled-environment growth cabinets until the 12-leaf stage, and subsequently, moved to a controlled-environment growth room. In the growth room, all the growth conditions were the same as that in the growth cabinets except the PPFD at the top of the canopy which was 350 μmol m^{-2} s^{-1}, and was supplied by a combination of fluorescent tubes and tungsten bulbs. Pots were weighed twice a week at the beginning of the experiment. The amount of water required to return the volumetric water content to that equivalent to an air-filled porosity (AFP) of 10% (volume air-filled

pores/total soil volume) was calculated from the pot weight, the weight of oven dry soil in each pot, the volume of the soil, the density of water and the estimated fresh weight of the plants. Adjustments for plant fresh weight at different leaf stages and days after sowing was estimated according to results of previously conducted physiological studies with maize under similar conditions (Tollenaar and Migus 1984, Tollenaar 1989, 1999).

The aeration status of the pots in the waterlogged treatment was characterized using measurements of the redox potential in the upper part of the rooting zone. No measurements were made to determine the extent to which these measurements reflected potentials at greater depths in the pots and therefore these measurements provide only an index of the average aeration status throughout the pot . Measurements were made daily at midday prior to the photosynthesis measurements using a combination Pt redox-reference electrode. The sand was removed from a given location in each pot, the electrode inserted 2.5 cm (i.e., about 5.5 cm below the free water surface), allowed to stabilize for 60 sec and the potential measured. Subsequent to the measurement the sand was replaced and a different location at the soil surface used for subsequent measurements.

6.4. Results and discussion

6.4.1. Drying treatment: critical water contents

The critical soil water contents (θ_{ll} and θ_t) for photosynthesis and transpiration varied among stages of development, whereas measurements of θ_{ll} and θ_t for whole plant transpiration were too variable to show significant effects (Table 6.1). The θ_{ll} and θ_t for leaf photosynthesis and transpiration declined from the 6- to the 12-leaf stage. The plant root system is present throughout the pot at the 12-leaf stage and, therefore, the critical water contents may be related to the size of the root system relative to the size of the pot. The critical water contents increased from the 12-leaf stage to the grain-filling period, although maize roots continue to increase in size until after silking (Tollenaar and Migus, 1984). The increase in critical soil water contents may be related to a decrease in the water uptake efficiency of the root system with the increase in the age of the roots.

Hybrid effects on the threshold content (θ_t), and the lower limit (θ_{ll}) for transpiration and photosynthesis were not significant (Table 6.2). The precision of most of the data presented in Table 6.2 was high and the data were consistent both across photosynthesis and transpiration measurements and across the two stages of development. The two maize hybrids used in this study have been shown to differ in their response to soil moisture stress (Nissanka et al., 1997), but results show that those differences are probably not attributable to the soil parameters measured in this study.

Conestogo and Fox soils differed substantially in respect to the free draining limit (θ_{fdl}), threshold content (θ_t), and the lower limit (θ_{ll}) for transpiration and photosynthesis (Table 6.3). Again, results were fairly consistent both across photosynthesis and transpiration and across three stages of development. The free drainage limit was about 0.15 m^3m^{-3} greater for the Conestogo than for the Fox soil, but the differences between the two soils for threshold content (θ_t) and the lower limit (θ_{ll}) were less than 0.15, resulting in significantly reduced intervals of θ_{fdl}-θ_{ll} and θ_{fdl}-θ_t for the Fox relative to the Conestogo soil.

6.4.2. Wetting treatment: redox potential

At the 15-leaf stage, saturation significantly affected the redox potential of soil during the whole stress period (Fig. 6.1). However, hybrid and soil effects were not significantly different. Redox potential followed a similar pattern over time for both the Pride 5 and Pioneer 3902 treatments grown in either Conestogo or Fox soil. The redox potential decreased from +350 mv at the 2nd day after saturation to approximately +25 mv at 10 days after saturation, then remained at +25 mv up to 17 days after saturation.

At silking, the redox potential decreased with time following an exponential curve for both the Pride 5 and Pioneer 3902 treatments (Fig. 6.2). Small differences were apparent immediately after saturation. Redox potential decreased from +300 mv for the Pride 5 treatment, whereas it decreased from +400 to approximately +200 mv within 4 days in the Pioneer treatment. Redox potentials were similar after 5 days of saturation for the two hybrids.

At grain filling, the redox potential for both hybrids responded similar to saturation, decreasing from +350 mv at 1st day of saturation to +150 mv at 10 days after saturation (Fig. 6.3).

6.4.3. Wetting treatment: transpiration and photosynthesis.

At the 6-leaf stage, the response of photosynthesis in Pride 5 and Pioneer 3902 to saturation were the same when grown in the Conestogo soil (Fig. 6.4). There were no changes within 2 days of saturation. However, a significant decrease was found starting on the 3rd day of saturation. When grown in the Fox soil (Fig. 6.5), no changes were found in the first 2 days. However, again, both Pride 5 and Pioneer 3902 decreased starting 3 days after saturation. Pioneer 3902 decreased faster than Pride 5 between 4 to 7 days after saturation.

At the 15-leaf stage, photosynthesis decreased at 6 days in Pride 5 while Pioneer 3902 decreased at 7 days after saturation when grown in the Conestogo soil (Fig. 6.6). Rates decreased at 4 days in Pride 5 while Pioneer 3902 decreased 5 days after saturation when grown in the Fox soil (Fig. 6.7).

At silking and during the grain-filling period, saturation had no effects on leaf photosynthesis of both hybrids up to 10 days after saturation (Figs. 6.8 and 6.9, respectively). However, many fine roots developed in upward direction in the bottom node in the later days of saturation. These newly developed roots probably compensated the saturation roots for absorption oxygen from soil, which alleviated the air limitation for the root system.

Similar trends were found for different stages based on leaf transpiration basis.

Piece-wise linear regression procedures (Statsoft 1999) applied to the rates of photosynthesis and the redox potential for the two soils and the two hybrids at the 15 leaf stage indicated that photosynthesis only began to decline when the redox potential fell below a critical value (Fig 6.10 and 6.11). Application of the piece-wise linear regression procedures to each rep showed that the mean critical redox potentials were significantly higher for Pride 5 than for Pioneer 3902 in each of the soils (152 versus 97 mv in the Conestogo soil and 237 versus 175 mv in the Fox soil). Studies in a separate project have indicated greater root shoot ratios in Pioneer 3902 and a larger root length may enable this hybrid to continue to maintain gas exchange rates up to lower oxygen levels. The critical redox potential was significantly higher in the Fox soil than in the Cambridge soil for each hybrid. The differences between soils may be due to differences in the content of readily reducible chemical species that may have an adverse effect on plant metabolism resulting in changes in gas exchange rates. An additional possible cause of the differences between soils may be differences in root length density. Further research is necessary to identify the reason for differences in the critical redox potential. An additional question, however, that is critically important to studies relating soil structure to plant response is to identify the structural characteristic(s) that have the greatest control on the time required to reach the critical redox potential when the water content is less than saturation.

6.5. Conclusions

The values of θ_{ll} and θ_t varied with maize growth stages. Early vegetative stage and reproductive stages had higher values of θ_{ll} and θ_t than later vegetative stages. Redox potential of both soils gradually decreased with increases in the duration of saturation. The effect of saturation on photosynthesis of both Pride 5 and Pioneer 3902 was evident only at 6 and 15 leaf stage, but was not detected at silking and grain filling stages for up to 10 days of saturation. Leaf photosynthesis for the two hybrids at the 15 leaf stage in both soils remained constant until the redox potential fell below a critical value. The critical redox potentials for Pride 5 were significantly higher than those for Pioneer 3902 in both soils and the critical redox potentials were higher in the Fox soil than the Conestogoa soil. Although the reasons for the differences the critical redox potential were not identified, these differences have important implications on the ability of the plants to withstand stress due to waterlogging and for identification of structural characteristics determining the time to reach the critical redox potentials at water contents lower than saturation.

6.6. Literature cited

Lipiec, J., T. Ishioka, A. Szustak, J. Pietrusiewicz, and W. Stepniewski. 1996. Effects of soil compaction and transient oxygen deficiency on growth, water use and stomatal resistance of maize. *Acta Agriculturae Scandinavica Section B - Soil Plant Sci.* 46: 186-91.

Lizaso, J. I., and J. T. Ritchie. 1997. Maize shoot and root response to root zone saturation during vegetative growth. *Agron. J.* 89: 125-34.

Nissanka, S.P., Dixon, M.A. and Tollenaar, M. 1997. Canopy gas exchange response to moisture stress in old and new maize hybrid. *Crop Sci.* 37:172-181.

Ray, J. D., and T. R. Sinclair. 1997. Stomatal closure of maize hybrids in response to drying soil. *Crop Sci.* 37: 803-7.

Tollenaar, M. and Migus, W. 1984. Dry matter accumulation of maize grown hydroponically under controlled-environment and field conditions. *Can. J. Plant Sci.* 64:475-485.

Tollenaar, M. 1989. Response of dry matter accumulation in maize to temperature. I. Dry matter partitioning. *Crop Sci.* 29: 1239-1246.

Tollenaar, M. 1999. Duration of the grain-filling period in maize is not affected by photoperiod and incident PPFD during the vegetative phase. *Field Crops Res.* 62: 15-21.

von Caemmerer, S. and G. D. Farquhar. 1981. Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves. *Planta* 153:376-387.

Table 6.1. Effects of different growth stages on θ_{ll} , θ_t based on photosynthesis, leaf transpiration and whole plant transpiration. The hybrid was Pioneer 3902 and the soil was Conestogo silt loam with a bulk density of 1.32 Mg m^{-3}.

Leaf Stages	Photosynthesis		Leaf transpiration		Whole plant transpiration	
	θ_{ll}†	θ_t†	θ_{ll}	θ_t	θ_{ll}	θ_t
6	0.149 a‡	0.266 a	0.138 ab	0.280 a	0.132 a	0.247 b
12	0.089 c	0.189 b	0.089 c	0.184 b	0.070 a	0.209 b
15	0.117 b	0.197 b	0.120 b	0.219 ab	0.116 a	0.200 b
silking	0.149 a	0.204 b	0.143 ab	0.226 ab	0.072 a	0.246 b
Grain-filling	0.162 a	0.199 b	0.188 a	0.225 ab	0.090 a	0.375 a

† θ_{ll} , θ_t: volumetric water content, m^3 m^{-3}

‡ Means with the same letter are not significantly different at 5% level according to Duncan's multiple range test.

Table 6.2. The response of two hybrids on $\theta_{fdl}-\theta_t$, $\theta_{fdl}-\theta_{ll}$, and $(\theta_{fdl}-\theta_t)/(\theta_{fdl}-\theta_{ll})$ at 15-leaf, silking and grain filling stages based on photosynthesis, leaf transpiration and whole plant transpiration. Pride 5 and Pioneer 3902 were grown in Conestogo silt loam at a bulk density of 1.32 Mg m^{-3}.

Stages	Hybrids	Photosynthesis				Leaf transpiration			Whole plant		
		θ_{fdl}†	$\theta_{fdl}-\theta_{ll}$†	$\theta_{fdl}-\theta_t$†	$(\theta_t-\theta_{ll})/(\theta_{fdl}-\theta_{ll})$ ‡	$\theta_{fdl}-\theta_{ll}$	$\theta_{fdl}-\theta_t$	$(\theta_t-\theta_{ll})/(\theta_{fdl}-\theta_{ll})$	$\theta_{fdl}-\theta_{ll}$	$\theta_{fdl}-\theta_t$	$(\theta_t-\theta_{ll})/(\theta_{fdl}-\theta_{ll})$
15-Leaf	Pride 5	0.485	0.362	0.280	0.230	0.367	0.222	0.400	0.387	0.241	0.378
	Pioneer	0.482	0.365	0.285	0.219	0.362	0.263	0.274	0.365	0.282	0.228
	LSD $_{(0.05)}$	0.011	0.001	0.094	0.037	0.037	0.073	0.120	0.021	0.080	0.108
Silking	Pride 5	0.475	0.328	0.284	0.138	0.333	0.281	0.157	0.423	0.197	0.536
	Pioneer	0.475	0.326	0.271	0.169	0.332	0.249	0.248	0.410	0.235	0.429
	LSD $_{(0.05)}$	0.001	0.023	0.048	0.091	0.001	0.086	0.126	0.099	0.010	0.152

† Volumetric soil water content, m^3 m^{-3}

‡ PAW_t

Table 6.3 Effects of different soils on the θ_{fdl}-θ_t, θ_{fdl}-θ_{ll}, and $(\theta_{fdl}$-$\theta_t)/(\theta_{fdl}$-$\theta_{ll})$ for Pioneer 3902 at 6-leaf, 12-leaf and 15-leaf stages grown in Conestogo silt loam (bulk density of 1.32 Mg m^{-3}) and Fox sandy loam (bulk density of 1.42 Mg m^{-3}).

Stages	Hybrids	Photosynthesis				Leaf transpiration			Whole plant transpiration		
		θ_{fdl}†	θ_{fdl}-θ_{ll}†	θ_{fdl}-θ_t†	$(\theta_t$-$\theta_{ll})/(\theta_{fdl}$-$\theta_{ll})$	θ_{fdl}-θ_{ll}	θ_{fdl}-θ_t	$(\theta_t$-$q_{ll})/(_{fdl}$-$\theta_{ll})$	θ_{fdl}-θ_{ll}	θ_{fdl}-θ_t	$(\theta_t$-$\theta_{ll})/(_{fdl}$-$\theta_{ll})$
6-Leaf	Conestogo	0.495	0.346	0.229	0.340	0.357	0.215	0.523	0.375	0.260	0.307
	Fox	0.372	0.314	0.167	0.472	0.319	0.155	0.395	0.302	0.283	0.062
	LSD $_{(0.05)}$	0.026	0.046	0.095	0.215	0.054	0.114	0.292	0.061	0.062	0.121
12-Leaf	Conestogo	0.494	0.401	0.303	0.246	0.402	0.306	0.405	0.423	0.285	0.325
	Fox	0.345	0.299	0.192	0.365	0.301	0.180	0.238	0.317	0.215	0.320
	LSD $_{(0.05)}$	0.033	0.032	0.050	0.187	0.019	0.084	0.287	0.125	0.291	0.140
15-Leaf	Conestogo	0.482	0.365	0.284	0.219	0.362	0.263	0.274	0.365	0.282	0.228
	Fox	0.371	0.295	0.223	0.245	0.281	0.200	0.274	0.297	0.232	0.217
	LSD $_{(0.05)}$	0.011	0.040	0.038	0.073	0.040	0.044	0.190	0.053	0.045	0.136

† Volumetric soil water content, m^3 m^{-3}

‡ PAW_t

Figure 6.1. Changes of soil redox potential with the duration of saturation at 15-leaf stage for Pride 5 and Pioneer 3902 (polynomial equation describing relation given in figure). Hybrids were grown at Conestogo and Fox soils.

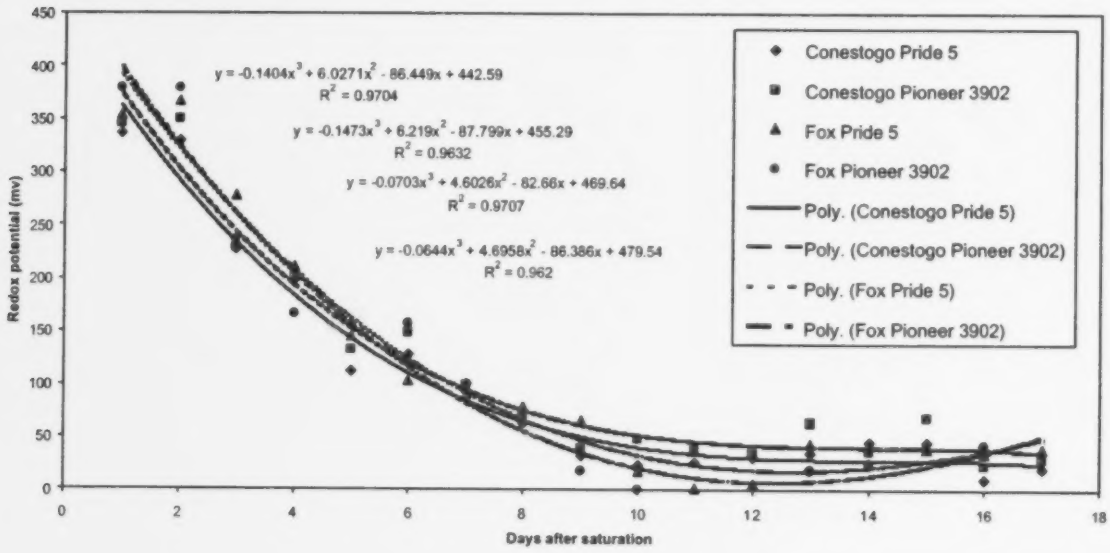


Figure 6.2. Changes of soil redox potential with the duration of saturation at silking stage for Pride 5 and Pioneer 3902 (logarithmic equation describing relation given in figure). Hybrids were grown in Conestogo soil.

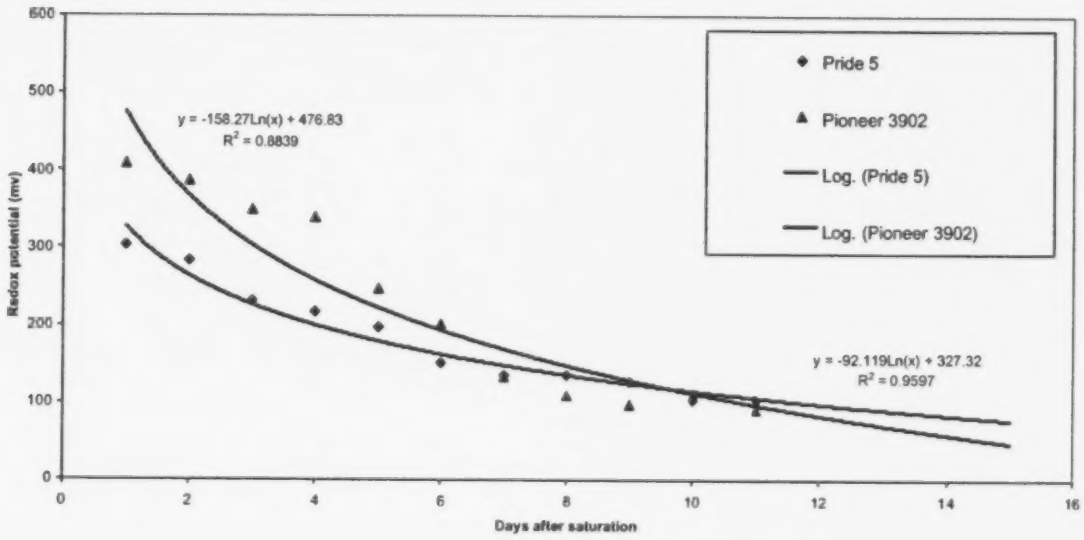


Figure 6.3 Changes of soil redox potential with the duration of saturation at grain-filling stage for Pride 5 and Pioneer 3902 (logarithmic equation describing relation given in figure). Hybrids were grown in Conestogo soil.

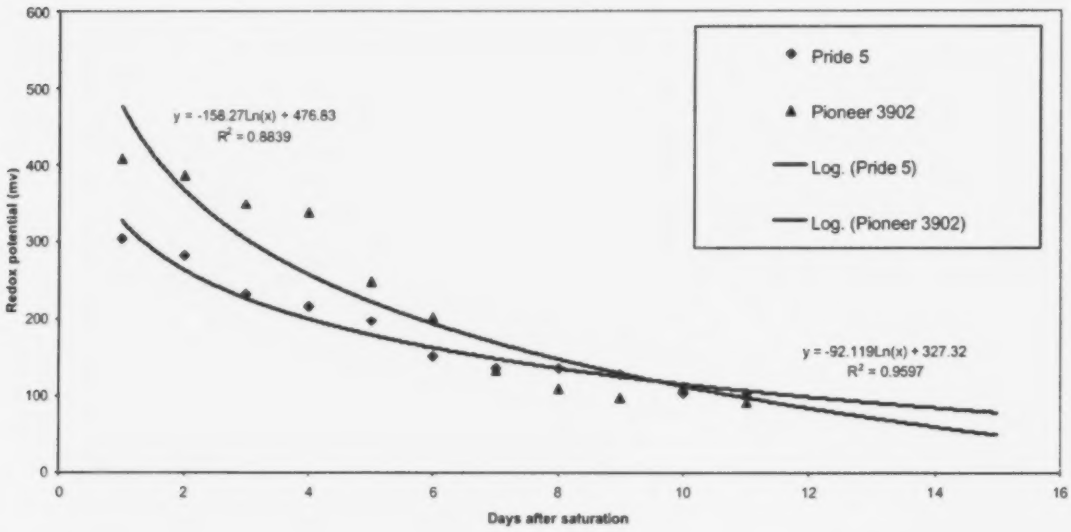


Figure 6.4 Photosynthesis of Pride 5 and Pioneer 3902 at 6th leaf stage at different periods of saturation in Conestogo silt loam soil (polynomial equation describing relation given in figure). Arrow indicates the day on which the saturation effect was identified.

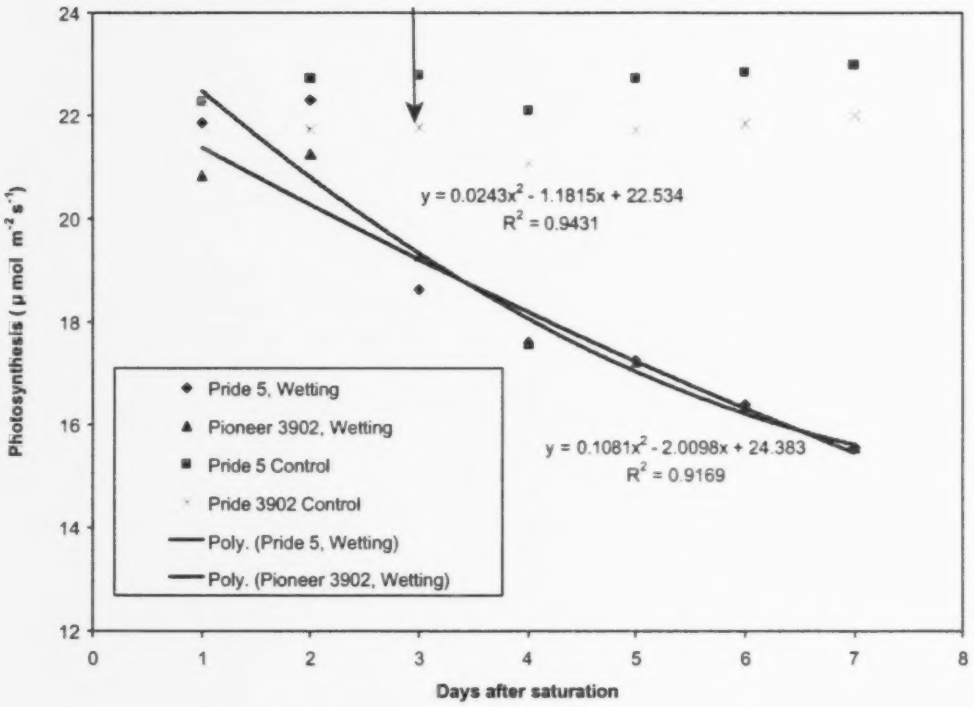


Figure 6.5 Photosynthesis of Pride 5 and Pioneer 3902 at 6th leaf stage at different periods of saturation in Fox sandy loam (logarithmic equation describing relation given in figure). Arrow indicates the day on which the saturation effect was identified.

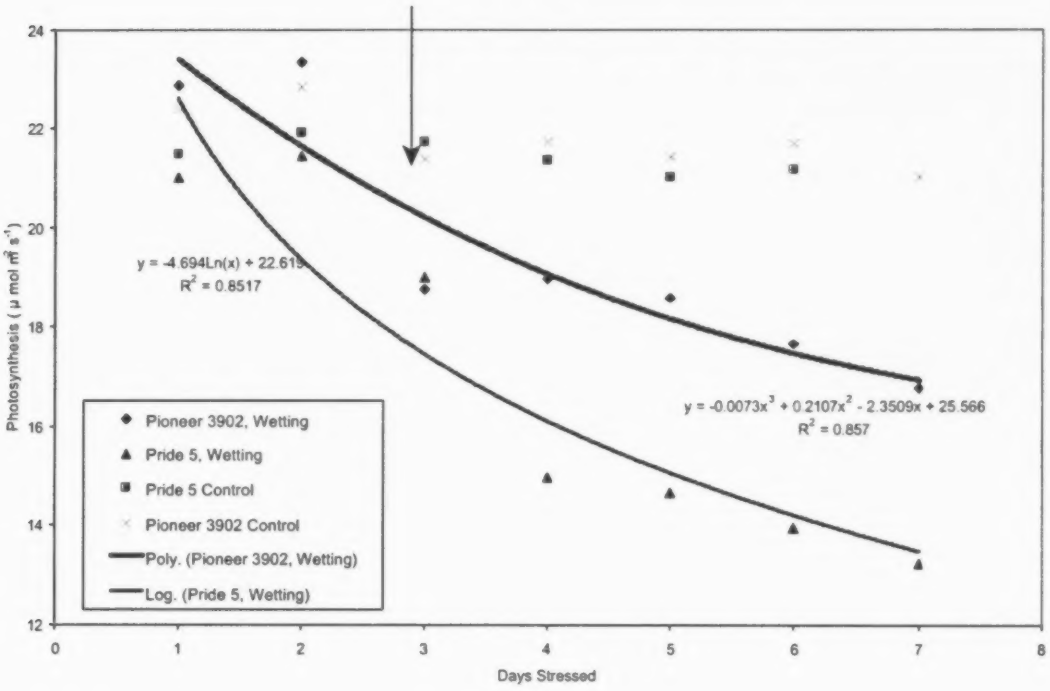

Photosynthesis (μ mol m² s⁻¹)
Days Stressed
y = -4.694Ln(x) + 22.615
R² = 0.8517
y = -0.0073x³ + 0.2107x² - 2.3509x + 25.566
R² = 0.857
Pioneer 3902, Wetting
Pride 5, Wetting
Pride 5 Control
Pioneer 3902 Control
Poly. (Pioneer 3902, Wetting)
Log. (Pride 5, Wetting)

Figure 6.6 Photosynthesis of Pride 5 and Pioneer 3902 at 15th leaf stage at different periods of saturation in Conestogo silt loam soil (polynomial equation describing relation given in figure). Arrow indicates the day on which the saturation effect became significant.

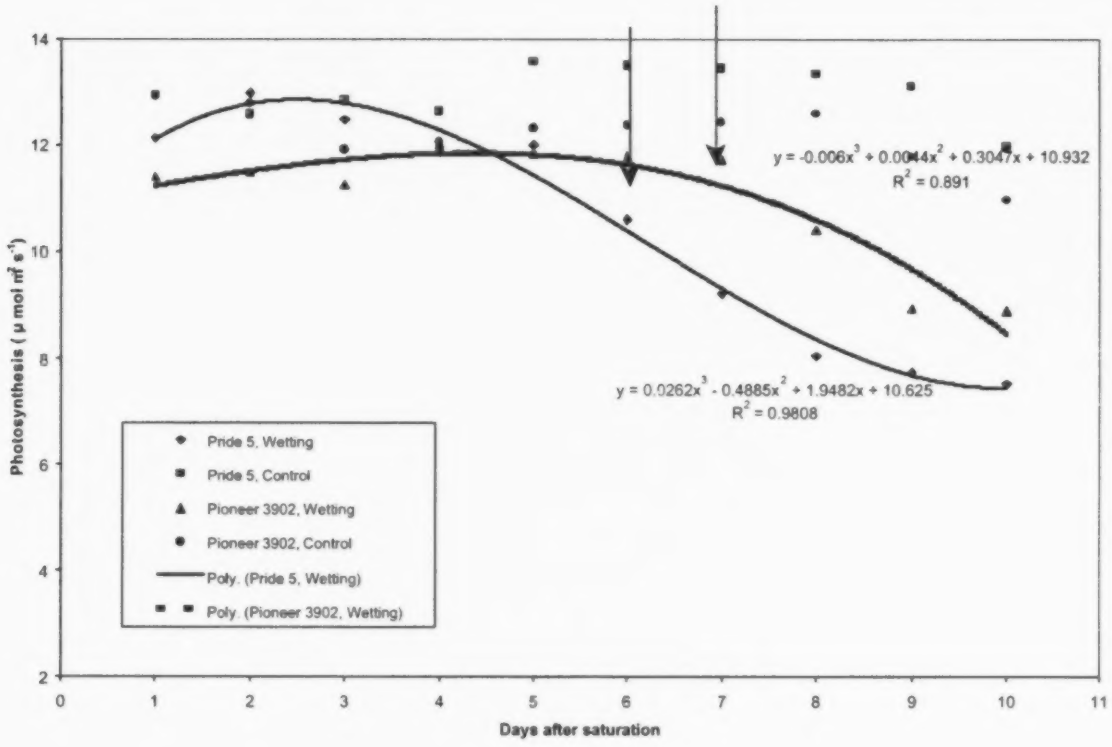

Photosynthesis (μ mol m² s⁻¹)
Days after saturation
y = -0.006x³ + 0.0044x² + 0.3047x + 10.932
R² = 0.891
y = 0.0262x³ - 0.4885x² + 1.9482x + 10.625
R² = 0.9808
Pride 5, Wetting
Pride 5, Control
Pioneer 3902, Wetting
Pioneer 3902, Control
Poly. (Pride 5, Wetting)
Poly. (Pioneer 3902, Wetting)

Figure 6.7 Photosynthesis of Pride 5 and Pioneer 3902 at 15th leaf stage at different periods of saturation in Fox sandy loam (polynomial equation describing relation given in figure). Arrow indicates the day on which the saturation effect became significant.

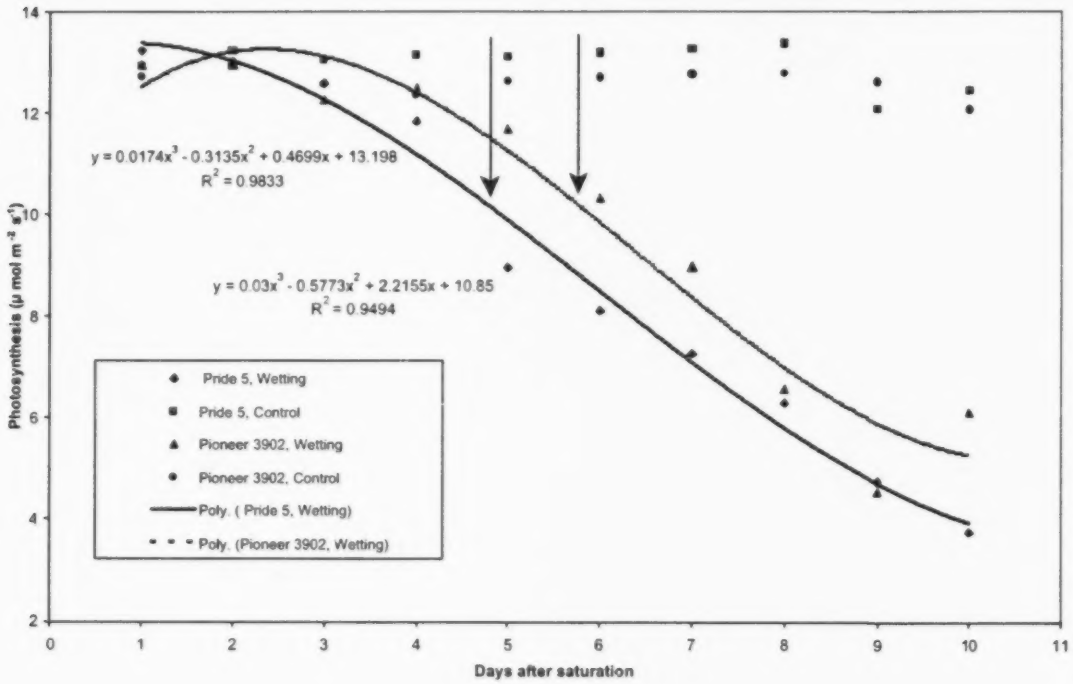


Figure 6.8 Photosynthesis of Pride 5 and Pioneer 3902 at silking at different periods of saturation in Conestogo soil (linear equation describing relation given in figure).

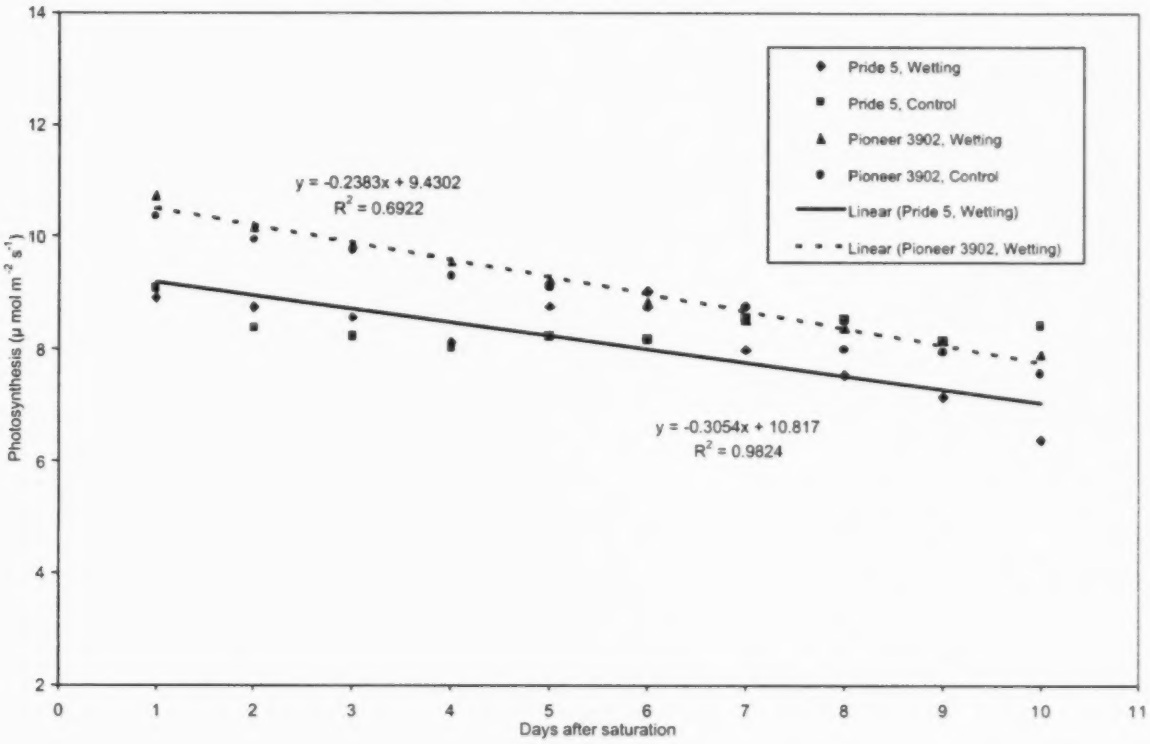


Figure 6.9 Photosynthesis of Pride 5 and Pioneer 3902 during grain-filling period at different times after saturation in Conestogo soil (linear equation describing relation given in figure).

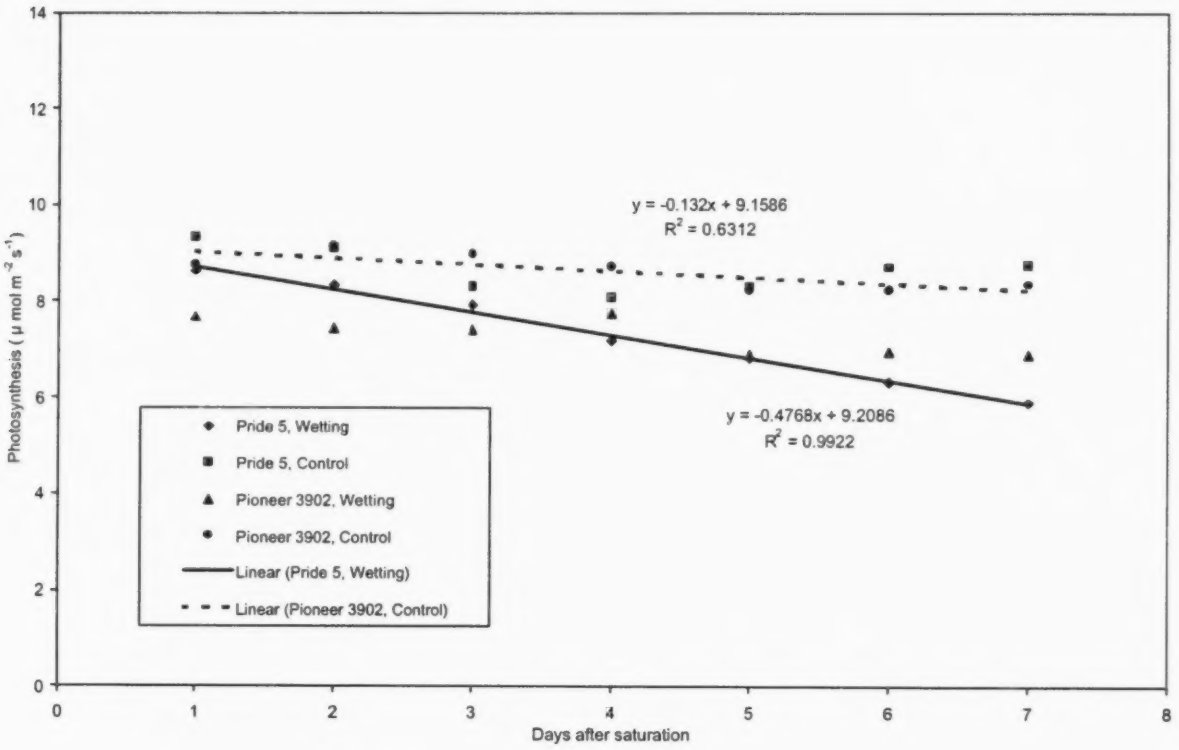
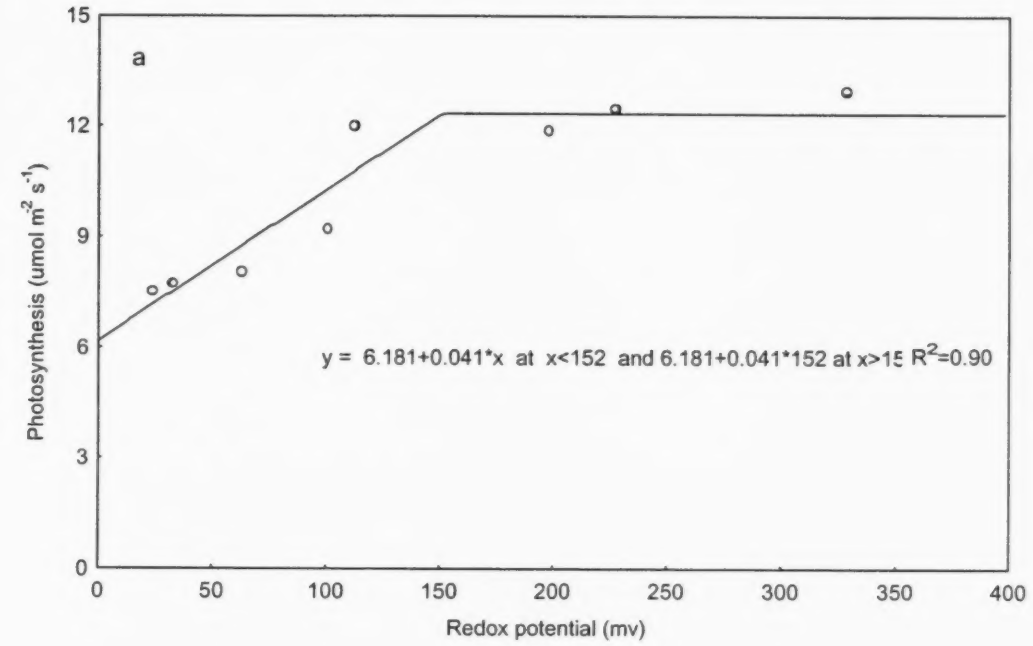


Fig. 6.10. Changes in rate of leaf photosynthesis with redox potential at 15th leaf stage for Pride 5 (a) and Pioneer 3902 (b) grown in Conestogo soil under saturated conditions.



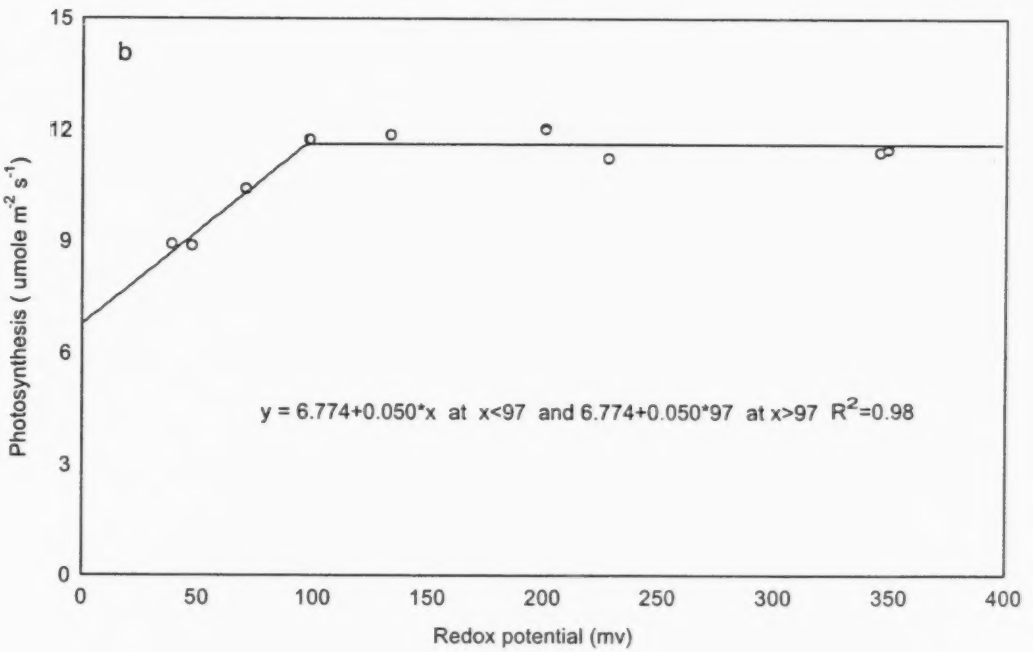
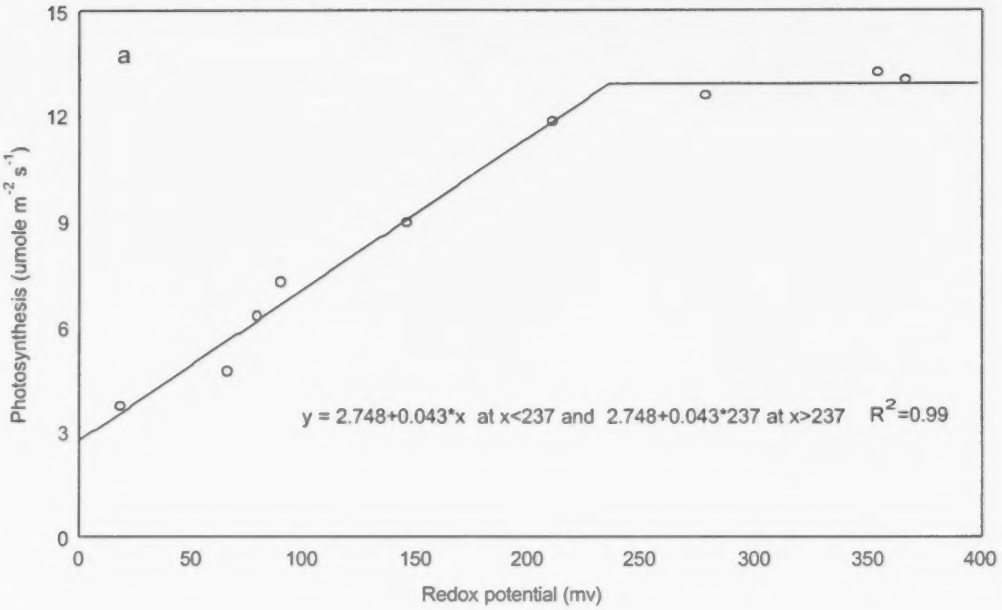
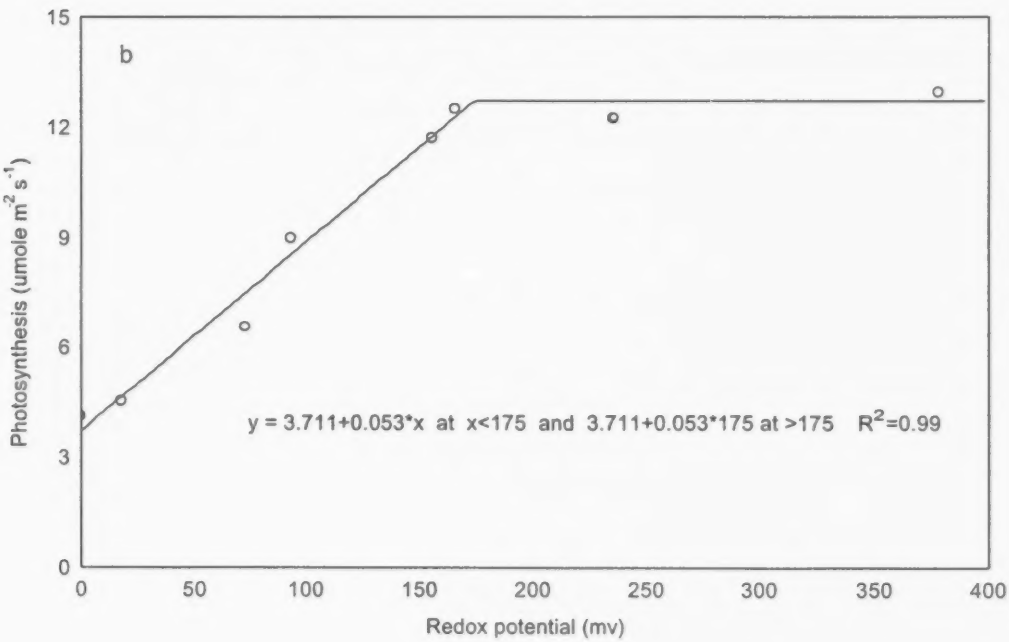


Fig. 6.11 Changes in rates of leaf photosynthesis with redox potential at 15-leaf stage for Pride 5 (a) and Pioneer 3902 (b) grown in Fox soil under saturated conditions.





7. Identification of critical water contents for the mineralization of legume nitrogen: effect of soil texture, organic carbon content and relative compaction

7.1. Introduction

Nitrogen (N) fertilizer requirement for crops can be estimated from the amount of N required by the crop, the sum of inorganic N present at planting, the net mineralization rate during the growing season and the amount of N losses through volatilization, leaching, and denitrification. Since inorganic N fertilizers make up >20 % of the operating expenses in corn production (Tollenaar, 1996), it is imperative that the N use efficiency be improved to increase net income and reduce environmental contamination. Mineralization of organic N from crop residues and soil organic matter can provide 30 to 100% of the crop requirement with the largest amount being provided when a legume is incorporated into the rotation. Nitrogen use efficiency is optimized when the rate of mineralization of organic N is synchronized with the uptake of N by the crop.

A soil N test has been developed and implemented in Ontario which permits estimation of the N requirement of corn based on the amount of inorganic-N present in the soil to 30 cm before side dressing (Kachanoski and Beauchamp, 1991). However, this test does not provide a measure of the N released from crop residues, manure addition, and legumes, especially when it is killed immediately prior to planting. Although ammonium and nitrate can be easily measured at planting time, there is a great deal of uncertainty with estimating the amount of N mineralized during the growing season. Plant growth and organic N mineralization often occur under conditions which do not correspond to optimal conditions, and the failure of the soil test to take these limiting conditions into account may account for poor correlations between soil test values (e.g. Herlihey, 1979) and plant-N (Rice et. al., 1995).

One best management practice which is being recommended to producers in Ontario is to include legumes, such as red clover and alfalfa in a rotation. Red clover in particular is an important cover crop in cereal-based rotations as it can be underseeded into cereal crops such as winter wheat and continue to grow after the wheat is harvested. Red clover has been found to increase the subsequent corn yields by improving soil structure, microbial activity, accelerating the decomposition of wheat straw (Drury et al., 1999) as well as providing organic N through N_2 fixation. The rate of N mineralization from red clover can be affected by the time (spring vs fall) and method (burn-down versus plowed) of control, soil temperature and texture, and perhaps soil water content (Vyn and Beauchamp, 1997). In conservation tillage systems crop residues are only partially incorporated. Hence the crop residue would not all have decomposed in the following spring when the subsequent crop is planted and the soil N test samples taken. A better understanding is required of the factors

which affect the mineralization rate of organic N or plant residue N to accurately estimate the crop fertilizer N requirements.

The mineralization of legume-N is also controlled by factors that regulate the mineralization of soil organic-N, although the relative importance of the factors may vary due to the physical location of the legume residue. The influence of factors, such as temperature, water content and aeration on the mineralization of organic-N have been well documented. Nitrogen mineralization is a biological process and therefore is affected by soil water contents. In very dry soil conditions, biological activity would be restricted, whereas in very wet conditions oxygen may be limiting the activity of aerobic bacteria. McKenney et al. 1995 found that N mineralization occurs under aerobic as well as anaerobic conditions. However when anaerobic conditions occur, nitrate can also be denitrified to nitric oxide and nitrous oxide. Hence the net amount of plant available N can be less than the amount of N mineralized. On the other hand, the effect of the soil matrix on mineralization has only recently begun to receive attention (e.g. Amato and Ladd, 1992). In a recent review, Jarvis et. al. (1996) have noted the need for more research on the influence of soil texture and structure on N mineralization.

Conservation tillage practices reduce plant residue incorporation and soil temperature and increase water content (Drury et al., 1999). A study of tillage practices in 8 Eastern Canadian soils reported that no-tillage soils were more compacted than conventional tillage soils (Angers et al., 1997) especially in the first few years after no-tillage was initiated. When soil was incubated under different levels of relative compaction at a constant water potential, it was found that N mineralization was related to aeration, residue-soil contact and pore size characteristics (Rasiah and Kay, 1997; 1999).

An innovative way to characterize the functional relation between N mineralization and water content in soils of different structure (which has not been used to date), would be to use critical water contents in the same manner as done for gas exchange measurements (chapter 5).

7.2. Objectives

The objectives of this study were to identify the critical water contents for N mineralization in soils of different structure and to assess the effects of legume addition on these water contents.

7.3. Materials And Methods

Five of the eight soils described in Table 4.1 were used in this study: #2, Brookston (Orthic Humic Gleysol); #4, Perth (Gleyed Grey Brown Luvisol); #5, Conestogo (Gleyed Orthic Melanic Brunisol); #7 Fox (Brunisolic Gray Brown Luvisol); and # Brady (Gleyed Brunisolic Grey Brown Luvisol). Soil samples were air-dried and crushed to pass through a 6 mm sieve.

Red clover (above ground biomass) was harvested in the fall of 1997, dried at 68 ± 2°C, and ground to pass a 1 mm sieve. The red clover residue contained 2.95% of N and 44.5% of organic C.

Treatments include five soil types (Table 7.1), eight water contents (20, 35, 50, 65, 80, 85, 90, and 95% of water filled pore space, WFPS), two levels of relative compaction (0.83 and 0.91) herein after referred to as low and high compaction treatments) which were representative of bulk densities associated with conventional- and no-tillage, two legume rates (0 and 100 mg N kg^{-1} soil, added using above ground red clover residue), and two decomposition stages (one and three months). The WFPS was calculated as the fraction of the total porosity that was water-filled. The incubation was arranged using a completely randomized design with three replicates. Soil samples without legume were also mixed in the same way as with legume amended samples to eliminate any differences in structure which result from the possible change in aggregate size during mixing.

Prepared soil samples were packed into aluminum rings (2.5 cm height and 4.8 cm diameter), and the water content was carefully adjusted using distilled and de-ionized water. Potassium nitrate was added to the soil in the aluminum rings, at a rate of 50 mg N kg^{-1} soil, to simulate N fertilizer addition at planting. The prepared aluminum ring was placed into a 265 cm^3 glass jar. The glass jar was covered with parafilm and four holes made to enable gas exchange to maintain an aerobic environment, while minimizing moisture loss from the jar. The water content was adjusted weekly. The soil rings were incubated in a growth chamber, which was held at 20 ± 2°C.

When the incubation was completed (i.e. after 1 or 3 months), the soil inside the incubation ring was removed and mixed. An equivalent of 10 g oven-dry soil samples were shaken with 100 mL KCl (2 *M*) for one hour, filtered though Whatman No. 40 filter papers and analyzed for mineral N (NH_4^+ and NO_3^--N+ NO_2^--N). Concentrations of NH_4^+-N and NO_3^--N + NO_2^--N, in extractant were determined using the Berthelot reaction for NH_4^+-N and the Cd reduction reaction for NO_3^--N + NO_2^--N on a TRAACS 800 autoanalyser (Tel and Heseltine, 1990).

Statistics analyses were performed using the proc GLM in SAS program (SAS Institute, 1996). Relationships between soil mineral N and WFPS or soil properties were determined using proc REG. The soil mineral N was related to WFPS using a quadratic function and then critical water contents defined, at the low and high end of the water content range, as the water contents at which soil mineral N at the end of the incubation period equals the initial value. A least limiting water range (LLWR) was calculated as the difference between the upper and lower critical values of WFPS or water contents. Hence, the LLWR is the range of WFPS when the net N mineralization is above zero.

7.4. Results and discussion

7.4.1. Soil mineral N

Extractable soil inorganic N was determined in the compaction and legume treatments at water contents equivalent to 20, 35, 50, 65, 80, 85, 90 and 95% WFPS (Figs. 7.1 - 7.5). The initial level of inorganic N in each soil at the start of the incubation was indicated by a horizontal line on the figures. This level includes the combination of the background and added (50 mg N kg^{-1}) inorganic N. Mineral N values above the line represent an increase in the amount of N mineralized, whereas values below the line represent a loss of mineral N. This loss was primarily due to denitrification (data not reported). Denitrification would be expected for the soils incubated at high WFPS (above 60%) which may create anaerobic microsites.

Soil type, relative compaction, and WFPS, as well as many interactions between these variables significantly affected levels of soil mineral N after both one and three months incubation (Table 8.2). Since there was a four way interaction between soil and other treatment factors, analysis of variance was conducted separately for each soil type (Table 7.3). A significant three way interaction between legume, compaction and WFPS occurred for all soils at both one and three months, with the exception of the Brady sandy loam soil. The Brady soil had a significant two way interaction between compaction and WFPS, as well as significant effects of legume addition on the soil mineral N levels.

The mineral N values after one month incubation for the Brady soil increased from 58.7 mg N kg^{-1} to a maximum value of about 81 mg N kg^{-1} for 35 to 65% WFPS treatments (Fig. 7.1). The mineral N values decreased substantially to values less than the initial mineral N contents for the small compaction treatments at WFPS values between 80 and 95%. This decrease was also evident for the large compaction treatments at the 90 and 95% WFPS. At three months, net mineralization was evident for all treatments between 20 and 80% WFPS with maximums occurring between 50 and 65% WFPS. In particular, the no-legume treatments had maximum mineral N values between 91 to 94 mg N kg^{-1} , whereas the legume treatments had maximum mineral N values of 108 mg N kg^{-1}. The mineral N values decreased for all treatments when the WFPS values were greater than 65%. Mineral N values were less than the initial amount for the small compaction treatments at 85-95% WFPS and for the large compaction treatments at 95% WFPS.

Net mineralization was considerably reduced for the Fox sandy loam at the one month incubation compared to the three month period (Fig. 7.2). After 3 months, the maximum amount of N mineralized increased from the initial level (61.2 mg N kg^{-1}) to 93 - 99 mg N kg^{-1} with legume addition and to 66 - 67 mg N kg^{-1} without legume addition. Net N mineralization occurred with the small compaction treatments between 20 and 65% WFPS and between 20 and 85% WFPS for the large compaction treatments.

Net N mineralization in the Conestogo loam soil (Fig. 7.3) followed a similar pattern as the Brady sandy loam soil (Fig. 7.1). The maximum amount of mineral N ranged from 112 to 114 mg N kg^{-1} after 1 month and from 112 to 128 mg N kg^{-1} after three months as compared to the initial value of 91.9 mg N kg^{-1}. After 3 months, the legume treatments had considerably more N mineralized than the non legume treatments, especially at the 50 and 65% WFPS levels, and for the large compaction and legume treatment at the 80% WFPS level. There was a dramatic decrease in mineral N at 95% WFPS levels, especially for the 2 legume treatments. Presumably the denitrifiers were using this soluble C source from the legume treatment to convert nitrate to NO, N_2O and N_2 and/or nitrate was being immobilized and converted to organic N.

There was, however, very little N mineralized with the Perth silt loam after 1 month (Fig. 7.4). Mineral N only increased to 70 mg N kg^{-1} with the non-legume treatments and to 86 mg N kg^{-1} with the legume treatments from the initial amount of 54 mg N kg^{-1}. Mineral N decreased from the initial concentrations at high WFPS levels, especially for the legume treatments. The Brookston clay loam soil also had reduced amounts of N mineralized at 1 month compared to 3 months (Fig. 7.5). At three months, mineral N increased to a maximum of 70 to 80 mg N kg^{-1} for the non-legume treatments and from 95 to 98 mg N kg^{-1} for the legume treatments from the initial value of 57 mg N kg^{-1}. It was interesting to note that in the Brookston soil, net mineralization occurred with all treatments for the 90 % WFPS and for the large compaction treatment at the largest WFPS value (95%), whereas all of other soils had either negligible mineral N values or mineral N contents that were less than the initial values.

7.4.2. LLWR and N Mineralization

Accumulative mineral N after one month incubation was quadratically related to WFPC in all soils except when red clover was added to the Brookston clay loam soil (Tables 7.4 and 7.5 and Fig. 7.1 to 7.5). When no red clover was added, the R^2 values ranged from 0.76 to 0.98. When red clover was added R^2 values ranged from 0.72 to 0.91 for all soils except the Brookston clay loam soil where the R^2 values were 0.67 for the small compaction treatment and a R^2 value of 0.44 for the large compaction treatment. After three months incubation, N mineralization was quadratically related to WFPS with significant R^2 values ranging from 0.68 to 0.92. The Perth soil had R^2 values ranging from 0.64 to 0.87.

The quadratic equations relating N mineralization to WFPS (Tables 7.4 and 7.5) were used to calculate both the upper and lower limits values of WFPS for net N mineralization (Table 7.6a). The LLWR was then calculated as the difference between the upper and lower limits. After 1 month incubation, the lower limit values ranged from 10 to 45% across all soils and treatments. In general, the lower limit values increased with increasing clay content, with the Brady sandy loam soil having the smallest values (10 to 24%) and the Brookston clay loam

soil having the largest values (27.2 to 45.2%). The lower limits increased for the large compaction treatments when compared with the small compaction treatments. The upper limits ranged from 52 to 98% across all soil types and treatments. The upper limit was also found to be largest with the Brookston soil and compaction increased the upper limit in all soils. The LLWR range varied between 28 to 69% across all soils and treatments. Compaction was found to increase the LLWR range. Hence WFPS affected net mineralization to different extents in the two compaction treatments.

After three months incubation the LLWR lower limits ranged between 13 to 40% across all soils and treatments (Table 7.6a). The lower limit was affected by soil type, with the Brady sandy loam having lower limits between 13 and 16 %, whereas the Brookston clay loam had lower limits between 19 and 40%. Compaction did not have as great an impact on the lower limit values after three months as it did after one month, with the exception of the Brookston soil amended with legume. The upper limits ranged from 68 to 100%, with the Brookston soil having the greatest values. Compaction increased the upper limits for all soils and legume treatments. The LLWR at three months ranged from 44% to 78% across all soils and treatments. Compaction increased the LLWR for all soils except the Brookston clay loam soil.

After one month, the large compaction treatment was quadratically related to sand content ($R^2 = 0.99$) with maximum LLWR values for soils with intermediate sand contents (Fig. 7.6). In the small compaction treatment, soils with both large and small sand contents also had lower LLWR values. The relationship between sand content and LLWR was not as evident after three months incubation.

The values of LLWR calculated on the soil volumetric water content basis (LLWR-V) (Table 7.7b) generally followed the same trend as those calculated using the fraction of water filled power space. In particular, the effect of red clover, as well as the effect of relative compaction without addition of legume at both one and three months and with addition of legume at one month were similar using both of these methods. At three months, LLWR-V was not as sensitive as LLWR to detect the effect of soil compaction.

Soil P appeared to be negatively related to LLWR for the small compaction treatment at both one and three months incubation with R^2 values of 0.94 and 0.91, respectively (Table 7.7a). Soil K was negatively related to the LLWR values for the legume addition at 3 months (R^2 values 0.96 to 0.98) and for the non-legume high compaction treatment after 1 month (R^2=0.99). After 1 month incubation, significant relationships existed amongst other soil properties and LLWR; however, the properties which were most important varied with compaction and legume treatment. Although soil nutrient availability affects biological activity, the relationship between soil nutrient status and LLWR was probably indirect. For example, the Fox soil had the greatest available P and the least LLWR in the non-legume small compaction treatments. The small LLWR was probably due to the lesser OC and clay + silt contents. Soils

with low OC and small clay + silt content would also be expected to have smallest P fixation capacity which may help to explain the large amount of available P.

Compared to LLWR, more soil property variables were found to be related to LLWR-V (Table 7.7b). However, the major contributing variables to LLWR-V were identical to those which affected LLWR, which include P when legume was not added and K when legume was added at three months. Other variables only accounted for a small portion of the variation in LLWR-V, ranging from 4 to 22%. With addition of legume at one month, over 92% of the variation in LLWR-V was accounted for by TN (total N) regardless of the level of soil compaction, whereas the causes of variation in LLWR varied depending on level of soil compaction.

7.5. Conclusions

Net N mineralization occurred in a restricted range of WFPS values. At small water contents, biological activity was restricted as the soil-water-organic matter contact was reduced. At large water contents, denitrification and/or immobilization converted the mineral N to N forms which are not plant available. Nitrogen mineralization was greater after 3 months of incubation compared to 1 month. Net N mineralization was increased when legumes were added especially for WFPS between 50 and 80%, whereas at WFPS values greater than 80%, the increased organic C inputs combined with the presence of anaerobic microsites may have enhanced denitrification losses (McKenney et al., 1995). The small compaction treatment did not increase the maximum amount of mineral N, but increased mineral N losses especially when the WFPS was greater than 80%. This study demonstrates that there is a range in water contents (LLWR) which enhance net N mineralization and would therefore affect the amount of plant available mineral N.

7.6. Literature cited

Amato, M. and J. N. Ladd. 1992. Decomposition of ^{14}C-labelled glucose and legume materials in soils: properties influencing the accumulation of organic residue C and microbial biomass C. Soil Biol. Biochem. 24:455-464.

Angers, D.A., Bolinder, M.A., Carter, M.R., Gregorich, E.G., Drury, C.F., Liang, B.C., Voroney, R.P., Simard, R.R., Donald, R.G., Beyaert, R.P., and J. Martel. 1997. Impact of tillage practices on organic carbon and nitrogen in cool, humid soils of Eastern Canada. Soil Tillage Res. 41:191-201.

Drury, C.F., Tan, C.S., Welacky, T.W., Oloya, T.O., Hamill, A.S. and S.E. Weaver. 1999. Red clover and tillage influence soil temperature, moisture and corn emergence. Agron. J. 91:101-108.

Herlihey, M. 1979. Nitrogen mineralisation in soils of varying texture, moisture and organic matter. Plant and Soil 53:255-267.

Jarvis, S. C., E. A. Stockdale, M. A. Shepherd, and D. S. Powlson. 1996. Nitrogen mineralization in temperate agricultural soils: processes and measurement. Adv. Agron. 57:187-235.

Kachanoski, R. G. and E. G. Beauchamp. 1991. Nitrogen soil test for corn. Unpublished report, Dept. Land Resource Sci., Univ. of Guelph.

McKenney, D.J., Wang, S-W., Drury, C.F. and W.I. Findlay. 1995. Denitrification, immobilization and mineralization in nitrate limited and non-limited residue amended soil. Soil Sci. Soc. Am. J. 59:118-124.

Rasiah, V. and B. D. Kay. 1997. Legume-N mineralization: effect of aeration and size distribution of water-filled pores. Soil Biol. Biochem. 30: 89-96.

Rasiah, V. and B. D. Kay. 1999. Temporal dynamics of microbial biomass- and mineral-N in legume amended soils from a spatially variable landscape. Geoderma 92: 239-256.

Rice, C. W., J. L. Havlin and J. S. Schepers. 1995. Rational nitrogen fertilization in intensive cropping systems. Fert. Res. 42:89-97.

Tel, D.A., and C. Heseltine. 1990.The analysis of KCl extracts for nitrate, nitrite and ammonium using a TRAACS 800 analyzer. Commun. Soil Sci. Plant Anal. 21:1681-1688.

Tollenaar, M. 1996. Corn production, utilization and environmental assessment. A review. Canada's Green Plan, AAFC..

Vyn, T. J. and E. G. Beauchamp. 1997. Enhancing assessment of red clover nitrogen availability to succeeding corn. URIF Contract Rept. 18 pp.

Table 7.1. Selected properties of soils used in the incubation study.

Soil classification	Clay	Silt	Sand	Organic C	Total N	C:N	pH	Soil Test P	Soil Test K	NH_4^+ + NO_3^--N
	---------- g kg^{-1} ----------							---------- mg kg^{-1} soil ----------		
Brady - sandy loam	46	307	647	26.2	1.99	13.2	7.7	11	63	10.6
Fox - loamy sand	69	167	764	13	0.64	20.3	6.9	55	120	17.2
Conestogo - loam	148	461	391	28.1	1.61	17.5	6.5	35	146	42.3
Perth - silt loam	267	493	240	15	0.99	15.2	7.7	13	126	8.3
Brookston - clay loam	378	351	271	18	1.54	11.7	7.5	24	206	10.3

Table 7.2. Statistical significance of soil type, legume addition, relative compaction, and fraction of water filled pore space (WFPS) on soil mineral N after 1 and 3 months incubation.

Factor	*P*	
	One month	Three months
Soil	**	**
Legume	**	NS
Compaction	**	**
Water Filled Pore Space (WFPS)	**	**
Soil x Legume	**	**
Soil x Compaction	**	**
Soil x WFPS	**	NS
Legume x Compaction	**	**
Legume x WFPS	**	**
RC x WFPS	NS	*
Soil x Legume x Compaction	**	**
Soil x Compaction x WFPS	**	**
Soil x Legume x WFPS	**	**
Legume x Compaction x WFPS	**	**
Soil x Legume x Compaction x WFPS		

*, **: significant at $P < 0.05$ and 0.01 levels, respectively. NS: not significant at $P < 0.05$ level.

Table 7.3. Statistical significance of soil type, legume addition, relative compaction, and water filled pore space (WFPS) on soil mineral N after 1 and 3 months incubation.

Factor	Brady sandy loam	Fox loamy sand	Conestogo silt loam	Perth silt loam	Brookston clay loam
			One month		
Legume	**	**	**	**	**
Compaction	**	**	**	**	**
WFPS	**	**	**	**	**
Legume x WFPS	NS	**	**	**	**
Compaction x WFPS	**	**	**	**	**
Legume x Compaction	NS	NS	NS	**	NS
Legume x Compaction x WFPS	NS	**	**	**	*
			Three months		
Legume	**	**	**	**	**
Compaction	**	**	**	**	
WFPS	**	**	**	**	**
Legume x WFPS	**	**	**	**	**
Compaction * WFPS	**	**	**	**	**
Legume x Compaction	NS	NS	*	*	NS
Legume x Compaction x WFPS	NS	**	*	**	**

*, **: significant at $P < 0.05$ and 0.01 levels, respectively. NS: not significant at $P < 0.05$ level.

Table 7.4. Relationships between mineral N and pore space water filled as a function of legume addition, soil relative decomposition stage in five tested soils.

Soil	No legume + low compaction				No legume + high compaction			
	a^b	*b*	*c*	R^2	*a*	*b*	*c*	R^2
One month								
Brady sandy	38.1	2.32	-0.0291	0.94**	8.27	3.15	-0.0307	0.84**
Fox loamy sand	43.6	1.19	-0.0164	0.94**	37.6	1.17	-0.0122	0.76*
Conestogo loam	49	2.95	-0.0336	0.98**	42.5	2.8	-0.0263	0.91**
Perth silt loam	40.2	0.85	-0.00846	0.94**	40.2	0.64	-0.00514	0.8*
Brookston clay	27	1.45	-0.0127	0.90**	38.6	0.576	-0.00215	0.86**
Three months								
Brady sandy	14.7	3.63	-0.0395	0.88**	27.2	2.67	-0.0253	0.79*
Fox loamy sand	20.2	2.33	-0.0254	0.90**	46.5	0.886	-0.00881	0.68*
Conestogo loam	35.1	3.49	-0.0357	0.88**	51.3	2.43	-0.0228	0.77*
Perth silt loam	26.3	1.62	-0.0145	0.64^+	36.1	0.992	-0.00758	0.74^+
Brookston clay	34.9	1.62	-0.0139	0.69^+	55	0.231	-0.000732	0.64^+

[a] Relative compaction of soils, at 0.83 and 0.91, respectively.

[b] N mineralization $= a + bWFPS + cWFPS^2$;

$^+$, *, **: Significant at 0.1, 0.05, and 0.01 levels, respectively.

^{NS} : Not significant at 0.1 level.

Table 7.5. Relationships between mineral N and pore space water filled as a function of legume addition, soil relative compaction (RC), and decomposition stage in five tested soils.

Soil	Legume + low compaction				Legume + high compaction			
	a[b]	*b*	*c*	R^2	*a*	*b*	*c*	R^2
One month								
Brady sandy loam	40.4	2.11	-0.0276	0.86**	-1.31	3.27	-0.0312	0.85**
Fox loamy sand	25.7	1.97	-0.0241	0.86**	2.52	2.96	-0.0291	0.74*
Conestogo loam	24.7	4.27	-0.0489	0.91**	-2.47	4.87	-0.046	0.72*
Perth silt loam	6.77	2.4	-0.026	0.84**	20.4	1.64	-0.0165	0.77*
Brookston clay	1.29	2.51	-0.0237	0.67^{+}	42.3	0.438	-0.00273	0.44^{NS}
Three months								
Brady sandy loam	2.5	4.6	-0.0489	0.92**	8.34	3.66	-0.0336	0.84**
Fox loamy sand	-11.9	4.46	-0.0459	0.92**	0.818	3.36	-0.0314	0.87**
Conestogo loam	-19.5	6.29	-0.0641	0.87**	-17.8	5.71	-0.053	0.72*
Perth silt loam	-16.9	3.99	-0.0404	0.87**	-21.6	3.79	-0.0343	0.65^{+}
Brookston clay	2.33	2.89	-0.0236	0.54^{NS}	29	0.96	-0.003489	0.92^{NS}

[a] Relative compaction of soils, at 0.83 and 0.91, respectively.

[b] N Mineralization $= a + bWFPS + cWFPS^2$;

$^{+}$, *, **: Significant at 0.1, 0.05, and 0.01 levels, respectively.

^{NS} : Not significant at 0.1 level.

Table 7.6a. Least limiting water range, calculated on the basis of fraction of water filled pore space, as a function of legume addition, soil relative compaction, and decomposition stage in five soils.

		One month			Three month		
		Lower limit	Upper limit	Range	Lower limit	Upper limit	Range
		%					
Low compaction	Brady sandy loam	10.2	69.6	59.4	14.4	77.5	63.1
	Fox loamy sand	20.4	52.3	31.9	23.7	68	44.3
	Conestogo loam	18.4	69.3	50.9	20.6	77.1	56.5
	Perth silt loam	20.4	80.1	59.7	21.1	90.7	69.6
	Brookston clay loam	27.2	86.1	58.9	19.3	97.8	78.5
High compaction	Brady sandy loam	19.9	82.8	62.9	13.5	92	78.5
	Fox loamy sand	28.9	66.9	38	20.9	89.6	68.7
	Conestogo loam	22.3	84.1	61.8	20.7	85.8	65.1
	Perth silt loam	27.7	96.7	69	21.6	96.8	75.2
	Brookston clay loam	37.8	98.3	60.5	21.5	99.2	77.7
Low compaction + legume Clover	Brady sandy loam	10	66.5	56.5	14.4	79.6	65.2
	Fox loamy sand	26.8	54.9	28.1	20.9	76.3	55.4
	Conestogo loam	20.6	66.7	46.1	23.1	75.1	52
	Perth silt loam	28.4	63.8	35.4	23.1	76.6	53.5
	Brookston clay loam	31.7	74.3	42.6	23.4	99.1	75.7
High compaction + legume	Brady sandy loam	23.7	81.5	57.8	16.2	92.8	76.6
	Fox loamy sand	27	74.7	47.7	22.9	84.2	61.3
	Conestogo loam	25.5	80.3	54.8	25	82.7	57.7
	Perth silt loam	28.8	70.5	41.7	26.1	84.3	58.2
	Brookston clay loam	45.2	93.1	47.9	39.8	99.8	60

Table 7.6b. Least limiting water range, calculated on the base of soil volumetric water content, as a function of legume addition, soil relative compaction, and decomposition stage in five soils.

		One month			Three month		
		Lower	Upper	Range	Lower	Upper	Range
		%					
Low compaction	Brady sandy loam	2.88	35.6	32.7	5.2	40.2	35
	Fox loamy sand	8.18	23.2	15	9.71	30.5	20.8
	Conestogo loam	7.08	34.7	27.6	8.28	38.5	30.3
	Perth silt loam	8.27	39.7	31.4	8.8	44.5	35.7
	Brookston clay	11.1	40.1	29	6.5	48.3	41.8
High compaction	Brady sandy loam	7.12	39.2	32.1	3.9	44	40.1
	Fox loamy sand	10.5	26.2	15.7	7.16	31.5	24.4
	Conestogo loam	7.89	38.6	30.7	7.04	39.7	32.6
	Perth silt loam	10.7	43.2	32.6	7.09	55.7	
	Brookston clay	17.5	45	27.5	5.05	45.05	40
Low compaction + legume Clover	Brady sandy loam	2.76	34	31.2	5.21	41.3	36.1
	Fox loamy sand	11.1	24.4	13.3	8.35	34.4	26
	Conestogo loam	8.22	33.3	25.1	9.63	37.6	28
	Perth silt loam	12.6	30.7	18.1	9.89	36.9	27
	Brookston clay loam	12.9	35.4	22.4	8.67	48.1	39.4
High compaction + legume	Brady sandy loam	9.09	38.3	29.2	5.24	44.3	39
	Fox loamy sand	9.72	29.4	19.7	7.96	33.5	25.6
	Conestogo loam	9.49	36.5	27	9.3	37.6	28.3
	Perth silt loam	11.2	30.9	19.8	9.89	37.4	27.5
	Brookston clay loam	18.9	49.9	31	14.6	48	33.4

Table 7.7a. Relationships between LLWR, calculated on the base of fraction of water filled pore space, and soil properties[□] after 1 and 3 month(s) incubation (excluding Brookston clay loam soil).

	No Legume added		Legume added (100 mg N kg^{-1})	
	Small Compaction	Large Compaction	Small Compaction	Large Compaction
One month				
	LLWR= 67.90 - 0.6109P R^2=0.94*	LLWR= 59.97 - 0.4640P +0.0374Mg R^2=0.99* (P:80%; Mg:19%)	LLWR=20.83 + 188.7TN - 0.03390K R^2=1.0** (TN:99%; K:1%)	LLWR= 41.80 + 6.707OC - 0.3839Clay R^2=0.99* (OC:74%; Clay:25%)
Three months				
	LLWR=66.45 - 0.4415P + 0.3388Clay R^2=0.99* (P:91%; Clay:8%)	LLWR= 22.54 + 7.669pH - 0.05056K R^2=0.99** (pH:95%; K:4%)	LLWR=75.40 - 0.1660K R^2=0.98**	LLWR= 91.33 - 0.2451K R^2=0.96*

[□] TN and OC are total nitrogen and organic carbon contents, respectively

[†],*, **; equation is statistically significant at $P < 0.1$, 0.05 and 0.01 levels, respectively.

[‡]; numbers in brackets indicate the relative contribution of each variable to the model, e.g. LLWR.

Table 7.7b. Relationships between LLWR, calculated on the base of soil volumetric water content, and soil properties after 1 and 3 month(s) incubation (excluding Brookston clay loam soil).

	No Legume added		Legume added (100 mg N kg^{-1})	
	Small Compaction	Large Compaction	Small Compaction	Large Compaction
One month				
	LLWR= 84.78 - 0.5104P - 6.050 pH R^2=0.99* (P:92%; pH:7.9%)‡	LLWR= 111.0 - 0.5590P - 9.351pH R^2=0.99† (P:80%; pH:19%)	LLWR=7.682 + 122.4TN - 0.01462K R^2=1.00** (TN: 99.7%; K: 0.3%)	LLWR= 9.473 + 93.06TN + 0.08259P R^2=0.99* (P:92%; TN:7%)
Three months				
	LLWR=39.70 - 0.3251P + 0.008673Mg R^2=0.99* (P:96%; Mg:4%)	LLWR= -19.81 - 1.278P + 5.611CN R^2=0.99† (P:86%; pH:14%)	LLWR= 66.70 - 0.1135K - 16.40Bulk density R^2=1.00** (K: 78%; Bulk density 22%)	LLWR= 34.80 - 0.1024K + 53.55 TN R^2=0.99* (P:77%; TN:22%)

†,*, **; equation is statistically significant at $P < 0.1$, 0.05 and 0.01 levels, respectively.

‡; numbers in brackets indicate the relative contribution of each variable to the model, e.g. LLWR.

Figure 7.1 Soil mineral N in the Brady sandy loam soil after one (a) and three (b) months incubation as affected by water filled pore space, relative compaction and legume treatments. Line indicated initial N content.

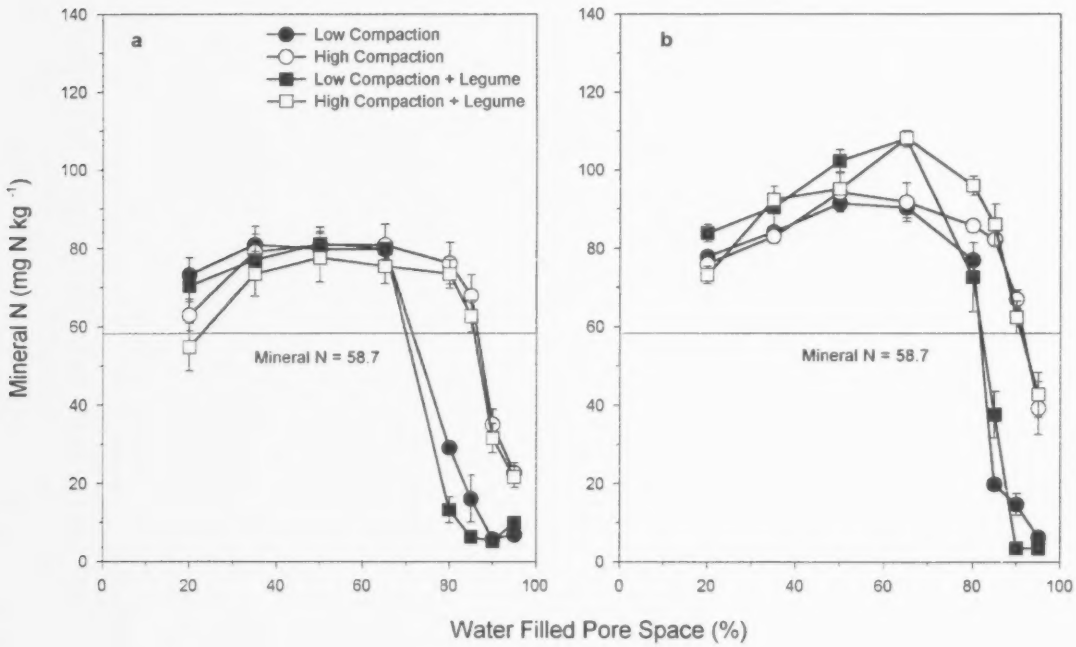


Figure 7.2 Soil mineral N in the Fox loamy sand soil after one (a) and three (b) months incubation as affected by water filled pore space, relative compaction and legume treatments. Line indicated initial N content.

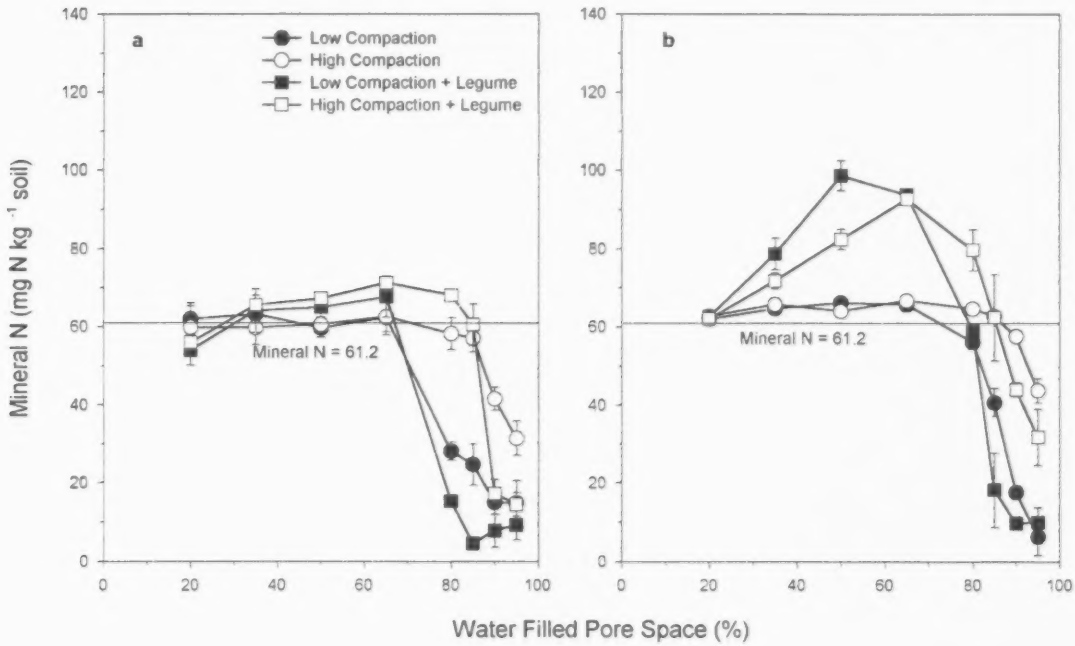


Figure 7.3 Soil mineral N in the Conestogo loam soil after one (a) and three (b) months incubation as affected by water filled pore space, relative compaction and legume treatments. Line indicated initial N content.

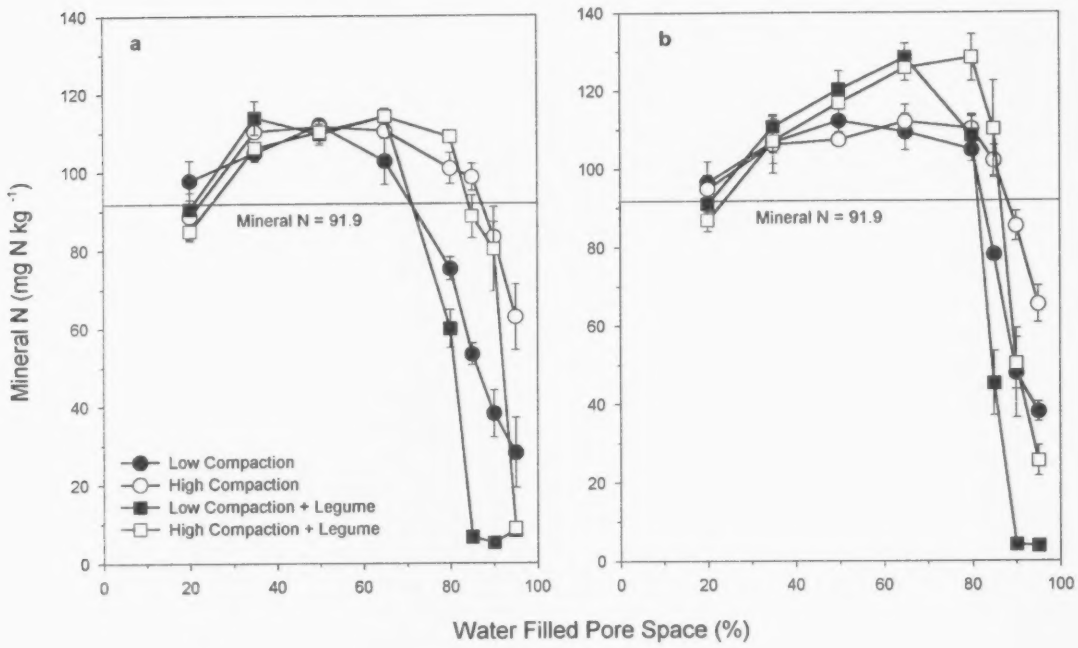


Figure 7.4 Soil mineral N in the Perth silt loam soil after one (a) and three (b) months incubation as affected by water filled pore space, relative compaction and legume treatments. Line indicated initial N content.

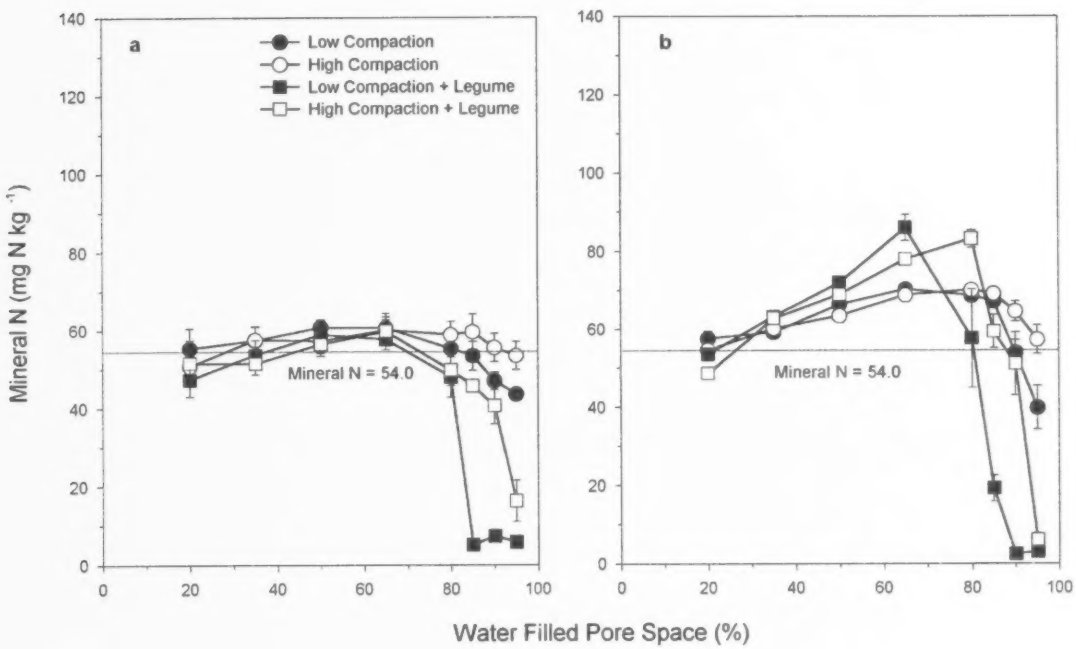


Figure 7.5 Soil mineral N in the Brookston clay loam soil after one (a) and three (b) months incubation as affected by water filled pore space, relative compaction and legume treatments. Line indicated initial N content.

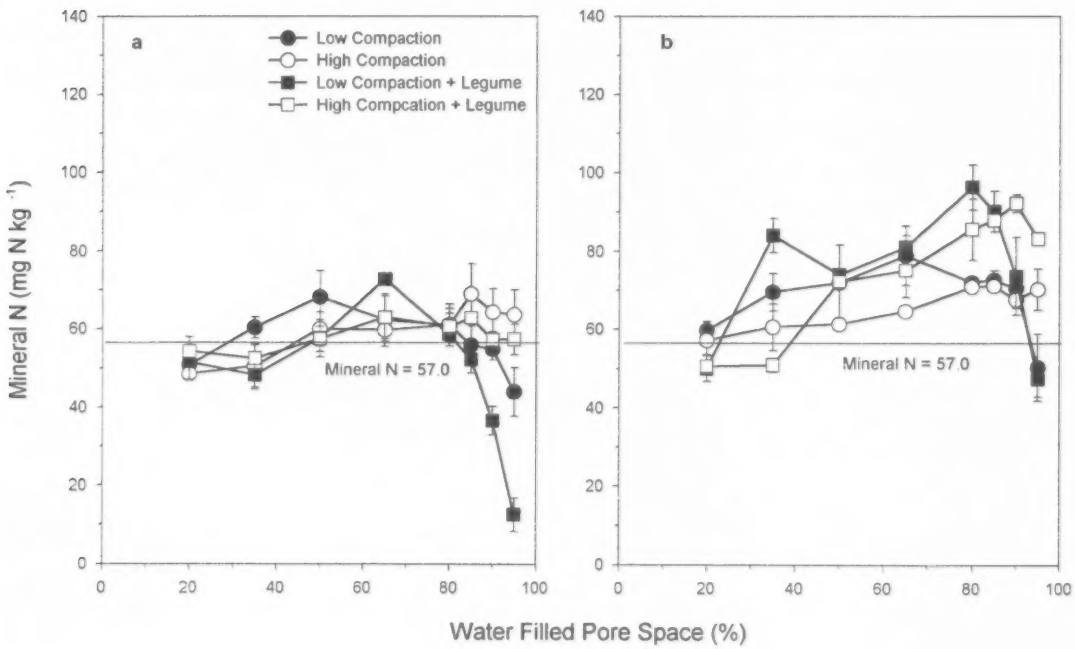
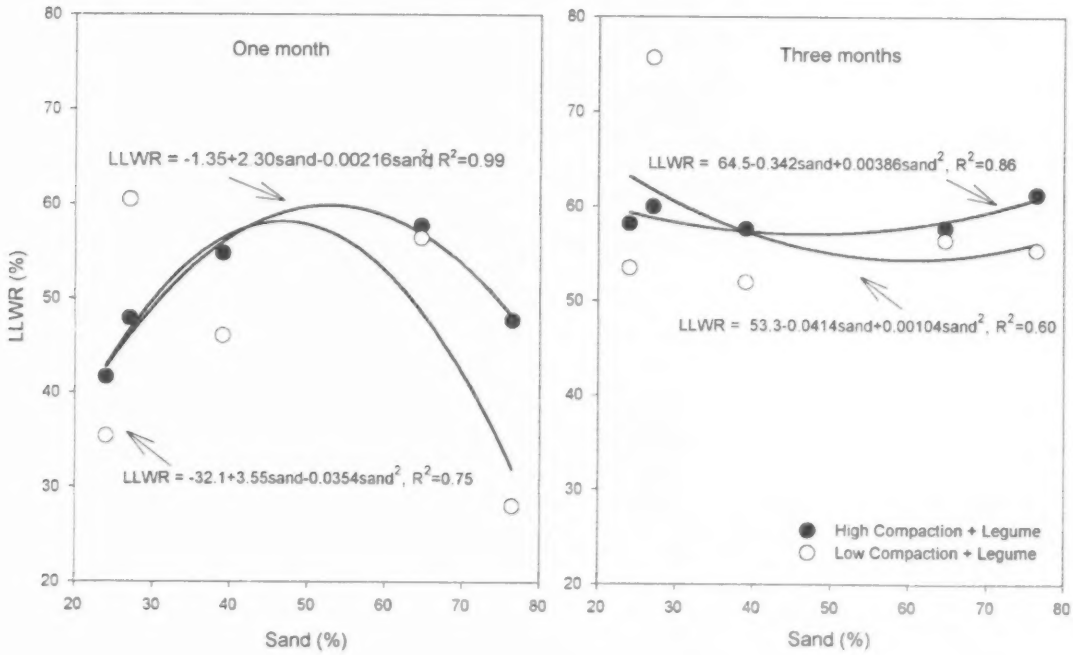


Figure 7.6 Relationships between sand content and the Least Limiting Water Range when legume was added at two relative compaction (RC) levels. Line indicated initial N content.



8. Comparison of critical water contents for gas exchange in plants and N mineralization by microorganisms and formulation of a combined least limiting water range

8.1. Introduction

The processes that contribute to characteristic critical water contents for gas exchange in plants are somewhat different from those for net N mineralization. Yet, under field conditions, plant response to variable water content in soils of different structure, may reflect both the direct influence of water content on gas exchange and the indirect influence of water content on N supply.

8.2. Objectives

The purpose of this chapter is to compare the critical water contents for gas exchange with those for N mineralization (identified in chapters 5 and 7 respectively) and to identify potential limitations in the use of these characteristic under field conditions.

8.3. Results and discussion

Fewer soils were used in the N mineralization study than in the gas exchange study and therefore comparisons of critical water contents were based on the soils used in the mineralization study.

The functional dependence of N mineralization was also different from that of gas exchange. The rates of gas exchange in a given soil, remained constant as the water content decreased from that of the control (an average air-filled porosity of 0.14 or a water-filled porosity of 0.86) to the threshold water content, θ_t, and then decreased rapidly to zero as the water content fell to θ_{ll}. At water contents greater than that of the control, the studies on two soils showed that the rates of gas exchange were not a unique function of water content but varied with the redox potential, which declined over time. In contrast, the net mineralization of N followed a quadratic relation with water content declining from a maximum value to zero at both low and high water contents. The functional dependence of net mineralization on water content was similar for incubations carried out over 1 and 3 months. The relations can be compared at critical water contents, i.e., the lower limits of both functions, the water content at the maximum net mineralization, and the θ_t of the gas exchange functions. The limits can also be combined to describe a least limiting range in water contents for crop growth.

8.3.1. Water contents at the lower limits

The water contents causing gas exchange in corn to cease (θ_{ll}) were generally greater than those causing net N mineralization to stop when the incubations did not include legume residue (Fig. 8.1). The exception to this generalization were the data from the Fox sand which lay above the 1:1 line implying that net mineralization in this soil ceased at water contents that were greater than those at which photosynthesis stopped. When legume was added prior to incubating the soils at different water contents, the water contents at the lower limit for photosynthesis and net N mineralization were generally similar (Fig. 8.2).

8.3.2. Water content at the maximum net mineralization and at the threshold water content, θ_t

The water contents at which maximum net mineralization occurred were always larger than θ_t, irrespective of legume treatment (Figs. 8.3 and 8.4). Net mineralization, expressed as a fraction of the maximum net mineralization, was always less than 1.0 at θ_t. The fraction did not vary with legume treatment although there was considerable variation among soils (from 0.56 to 0.98). The fraction, averaged across soils and legume treatments, was 0.67. While values of the fraction that were substantially less than 1.0 at θ_t may have little consequence in soils to which sufficient inorganic fertilizer has been added to meet crop requirements, it may impose limitations where the N mineralized from organic sources is a significant source of the required N.

The water contents at maximum net mineralization were always less than field capacity (-0.01 MPa).

8.3.3. Water contents at the upper limit of net mineralization

Under field conditions, the importance of the water content at the upper limit of net mineralization depends on its value relative to field capacity. A comparison of field capacity with the water contents at the upper limit of net mineralization indicates that field capacity was often greater than the water content at zero net mineralization when no legume residue was present (Fig. 8.5), particularly for 1 month incubation. Similar results were found for soils that were incubated with legume residue (Fig. 8.6). Soils with data points lying below the 1:1 line would experience a net loss of N if the soil water content remained at field capacity. The data for 1 month incubation may be most relevant to conditions after tillage early in the growing season.

8.3.4. Least limiting water range

A least limiting water range for plant growth may be defined utilizing critical water contents derived from measurements of gas exchange and/or net N mineralization. The lower limit would coincide with the lower limit for gas exchange (θ_{ll}), since this limit was generally equal to or greater than the lower limit for net mineralization. In the absence of definitive critical water contents for limiting aeration conditions obtained from gas exchange measurements, the upper limit in a least limiting water range may be obtained from the net mineralization and field capacity measurements. The upper limit would be defined as the water content at field capacity or the water content at which net mineralization is zero, which ever is smaller.

Da Silva and Kay (1997) estimated the lower limit of the least limiting water range as the larger of either the water content at the permanent wilting point (1.5MPa) or the water content at a soil resistance to penetration of 2 MPa. A comparison of this estimation of the lower limit for with θ_{ll} for gas exchange in chapter 5 indicated that the lower limit for penetration resistance was significantly greater than 2 MPa.

Da Silva and Kay (1997) estimated that the upper limit of the least limiting water range for plant growth would coincide with the smaller of the water contents at either field capacity or 10% air-filled porosity. Values of the upper limit calculated using this approximation are compared with those using the upper limit based on either field capacity or the upper limit of net N mineralization in Fig 8.7. At large values of the upper limit (finer textured soils), the approximation overestimates the limit when data from 1 month incubation were used but underestimates the limit for these soils when data from 3 month incubation are used. Use of the smaller of either field capacity or the air-filled porosity of 10%, therefore, appears to be reasonable as an approximation of the upper limit of the least limiting water range for plant growth.

Values of the least limiting water ranges (LLWR), calculated using the water contents at which gas exchange ceases and the upper limits based on either field capacity or the water content at which net mineralization is zero, are given in Table 8.1. Multiple regression analyses (forward stepwise) were used to identify the soil properties from among relative compaction, clay, silt and OC contents, and OC/clay that were most strongly correlated with LLWR. Applying these techniques to the data in Table 8.1 gave the following:

$$LLWR = -0.220 + 0.006\ silt + 0.262\ OC/clay + 0.405\ RC - 0.044\ OC - 0.002\ clay \qquad 8.1$$

$$N=10,\ R^2=0.97$$

The relation between values of the LLWR, given in Table 8.1, are related to clay content and relative compaction in Fig. 8.8. Three features of these data are noteworthy. First,

the combination of clay and silt content terms in Eqn. 8.1 reflect the curvilinear relation of the LLWR with clay content. Second, the LLWR is larger for greater compaction. Both the upper and the lower limits increased with increasing compaction but the upper limit increased a larger amount than the lower limit. This result was consistent across all soils but unexpected since conventional wisdom suggests that denitrification is enhanced in compacted soils and therefore the upper limit would have been expected to occur at lower water contents. Finally, the large value of the LLWR for the coarsest textured soil reflects the large OC content of this soil relative to that of the soil with 7% clay (Fox).

The studies, upon which the preceding comparison was based, were necessarily based on soils that had been sieved and repacked. These soils were not structurally identical to their corresponding states under field conditions and therefore the absolute value of the critical water contents would not be expected to be identical to values measured in undisturbed soils. In addition. both gas exchange and net N mineralization are temperature dependent and there is no information on the extent to which the critical water contents may vary within the range in soil temperatures commonly encountered in Ontario during the growing season.

8.4. Conclusions

Although somewhat different processes contribute to the characteristic critical water contents for gas exchange in plants and net N mineralization by microorganisms, the water contents can be related. The lower critical water contents at which net N mineralization was zero were generally similar to, or lower than, those at which gas exchange ceased. In the absence of a well defined upper critical water content for gas exchange, an upper limit for plant growth may be defined on the basis of the smaller of either field capacity or the water content at zero net N mineralization. The difference between these upper and lower critical water contents represents a least limiting water range (LLWR). The upper and lower limits and the LLWR were more strongly correlated with soil properties related to texture, OC and relative compaction than to derived characteristics such as water potential, soil resistance to penetration, and air-filled porosity.

8.5. References cited

da Silva, A. P. and B. D. Kay. 1997. Estimating the least limiting water range of soils from properties and management. Soil Sci. Soc. Amer. J. 61: 877-883.

Table 8.1 Critical water contents from gas exchange and net N mineralization measurements (1 month incubation without legume) used to define a non-limiting water range.

Soil	Clay content (%)	Organic carbon content (%)	Bulk density (Mg m^{-3})	Lower limit water content from photosynthesis, q_{ll} (m^3 m^{-3})	Water content at upper limit net mineralization (m^3 m^{-3})	Field capacity, -0.01MPa (m^3 m^{-3})	Least limiting water range (m^3 m^{-3})
Brookston	40.6	1.89	1.38	0.187	0.450	0.484	0.263
	40.6	1.89	1.26	0.166	0.401	0.455	0.235
Perth	27.2	1.50	1.40	0.118	0.432	0.432	0.314
	27.2	1.50	1.28	0.107	0.397	0.402	0.290
Conestogo	15.3	2.81	1.33	0.081	0.386	0.489	0.305
	15.3	2.81	1.21	0.093	0.347	0.444	0.254
Fox	7.0	1.30	1.55	0.046	0.262	0.268	0.216
	7.0	1.30	1.41	0.044	0.232	0.252	0.188
Brady	5.5	2.62	1.30	0.073	0.392	0.413	0.319
	5.5	2.62	1.19	0.067	0.356	0.362	0.289

Figure 8.1 Water contents at which photosynthesis and net mineralization of N in soils without added legume cease.

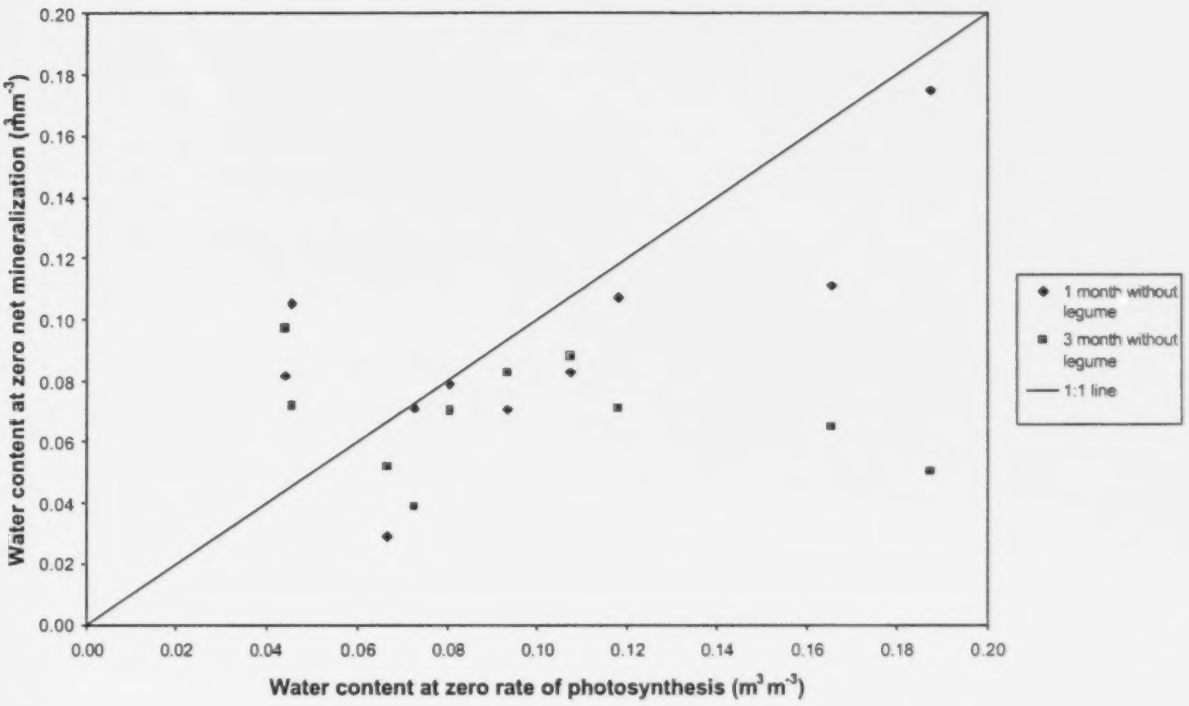


Figure 8.2 Water contents at which photosynthesis and net N mineralization in soils with added legume cease

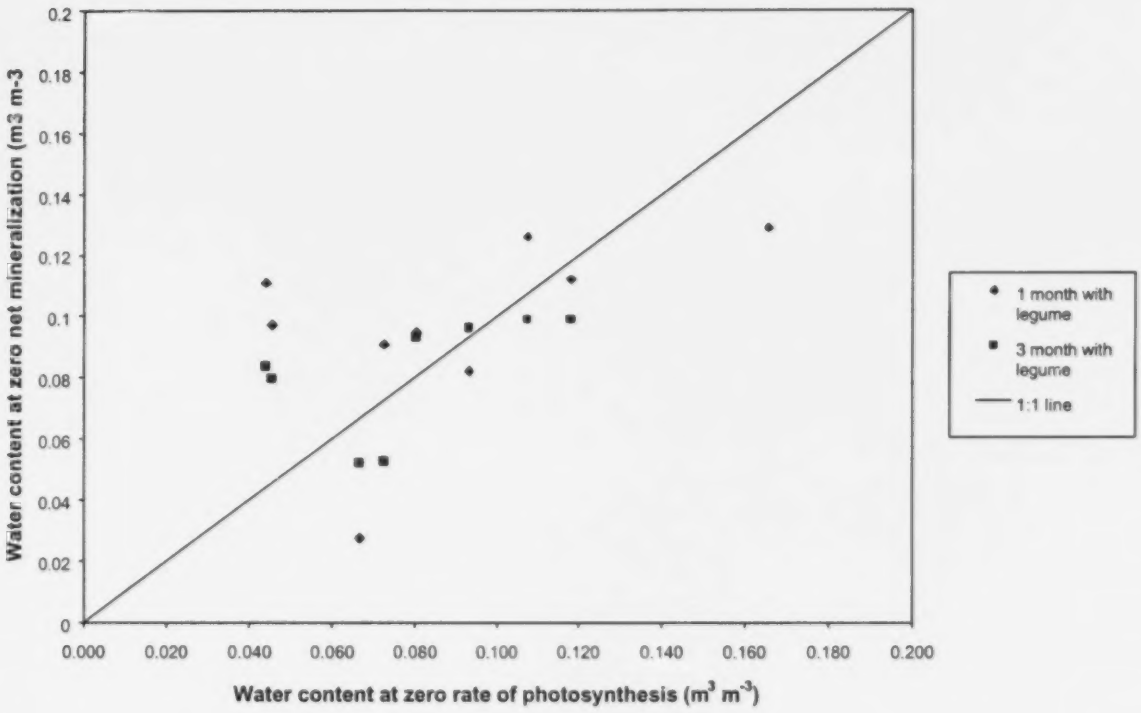


Figure 8.3 Relation of water content at maximum net N mineralization, without added legume residue, to threshold water content for photosynthesis.

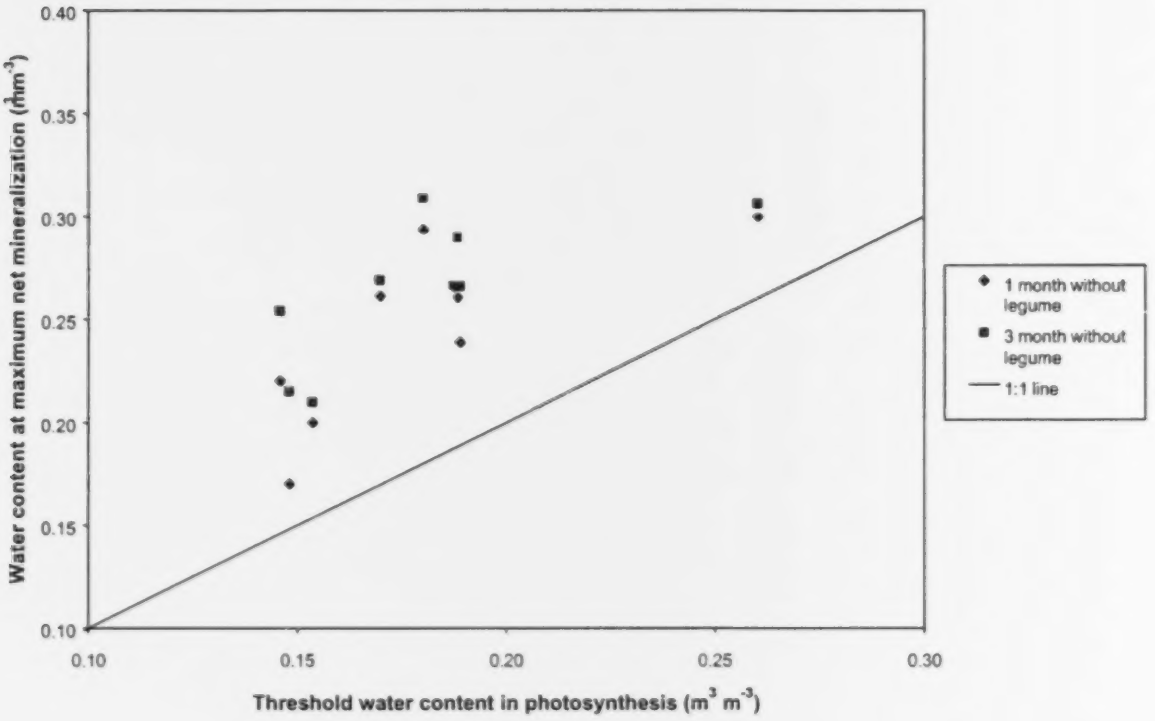


Figure 8.4 Relation of water content at maximum net mineralization, with added legume residue, to threshold water content for photosynthesis.

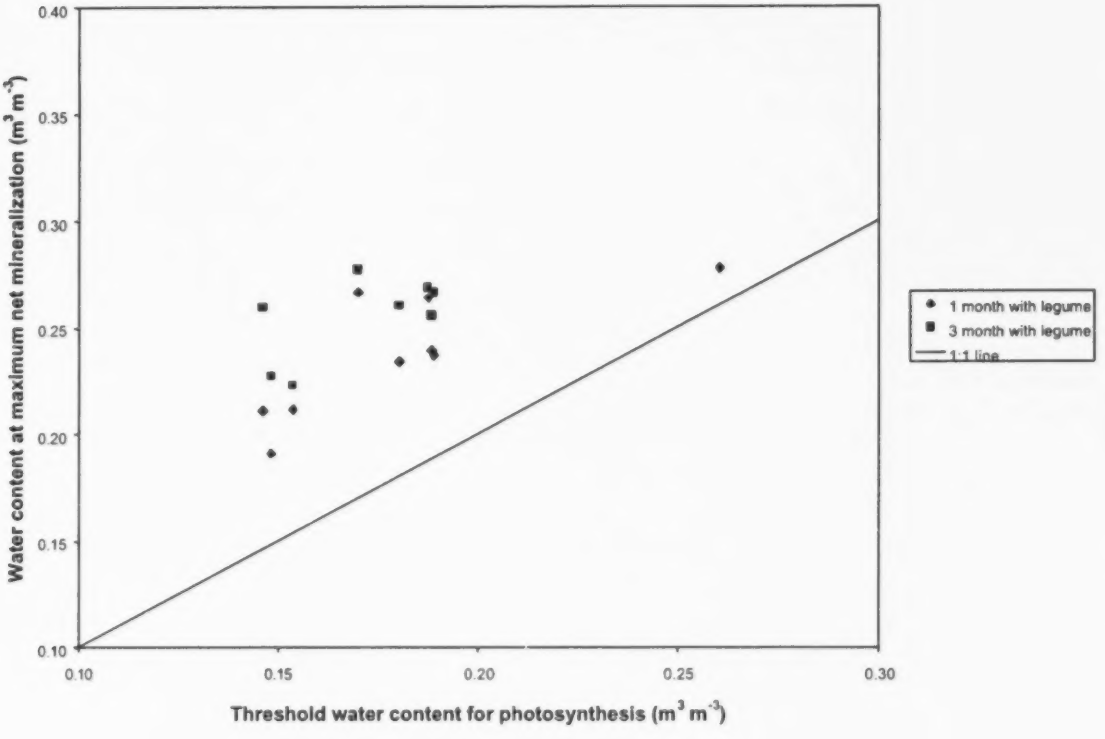


Figure 8.5. Comparison of the water content at field capacity (taken from the water release curve at -0.01 MPa) and the water contents at which net N mineralization is zero (soils without added legume) that were incubated for 1 and 3 months.

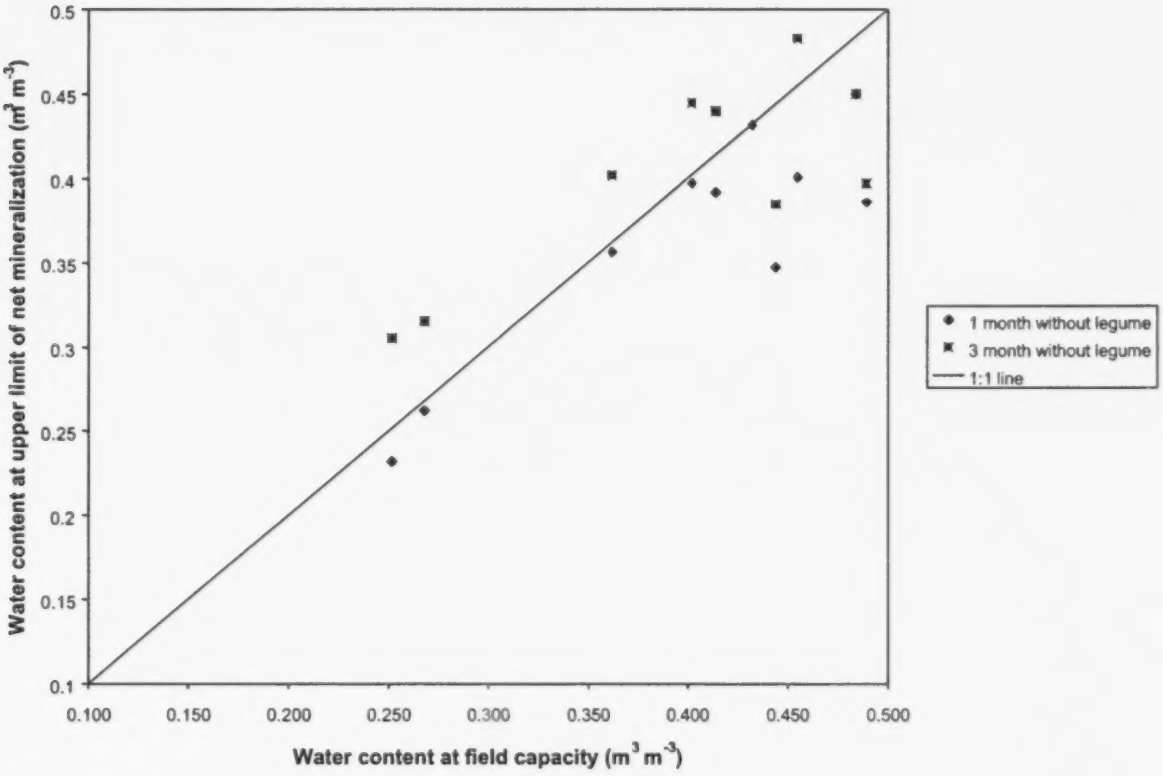


Figure 8.6. Comparison of the water content at field capacity (taken from the water release curve at -0.01 MPa) and the water contents at which net N mineralization is zero (soils with added legume) that were incubated for 1 and 3 months.

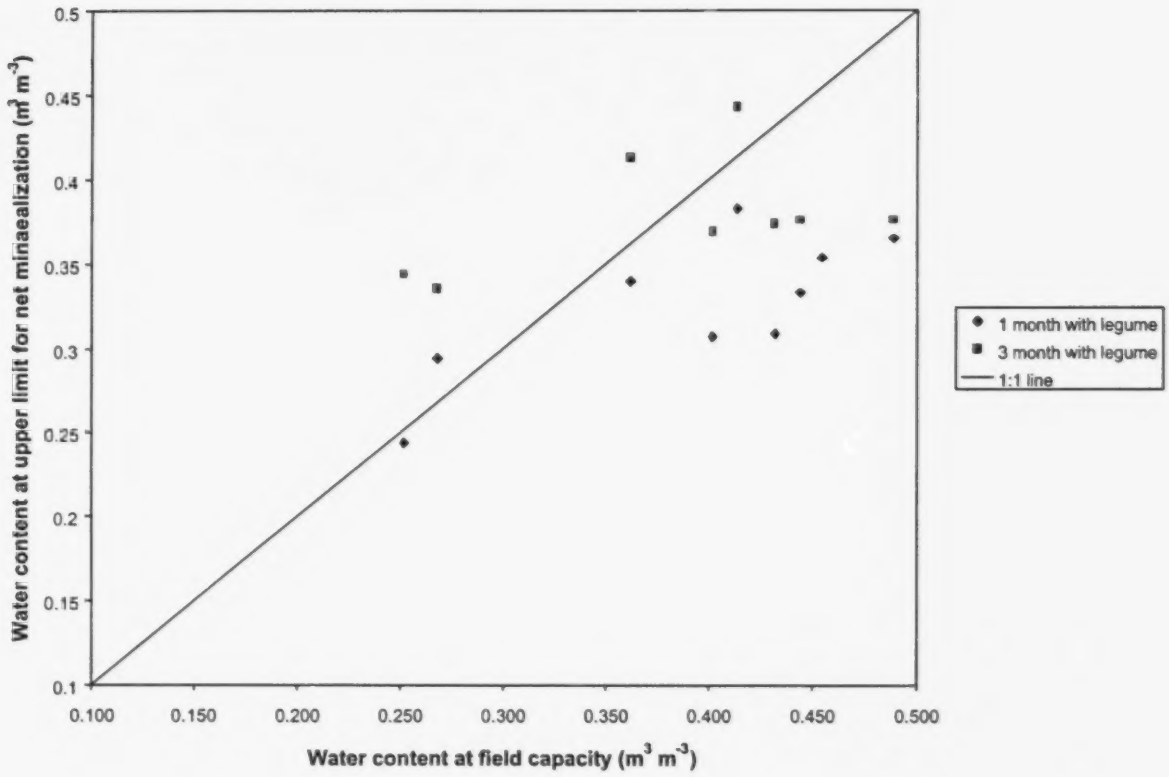


Figure 8.7 Comparison of upper limit of LLWR calculated from the smaller of field capacity (FC) or the water content at zero net N mineralization with that calculated from the smaller of FC and the water content at 10% air-filled porosity (AFP)

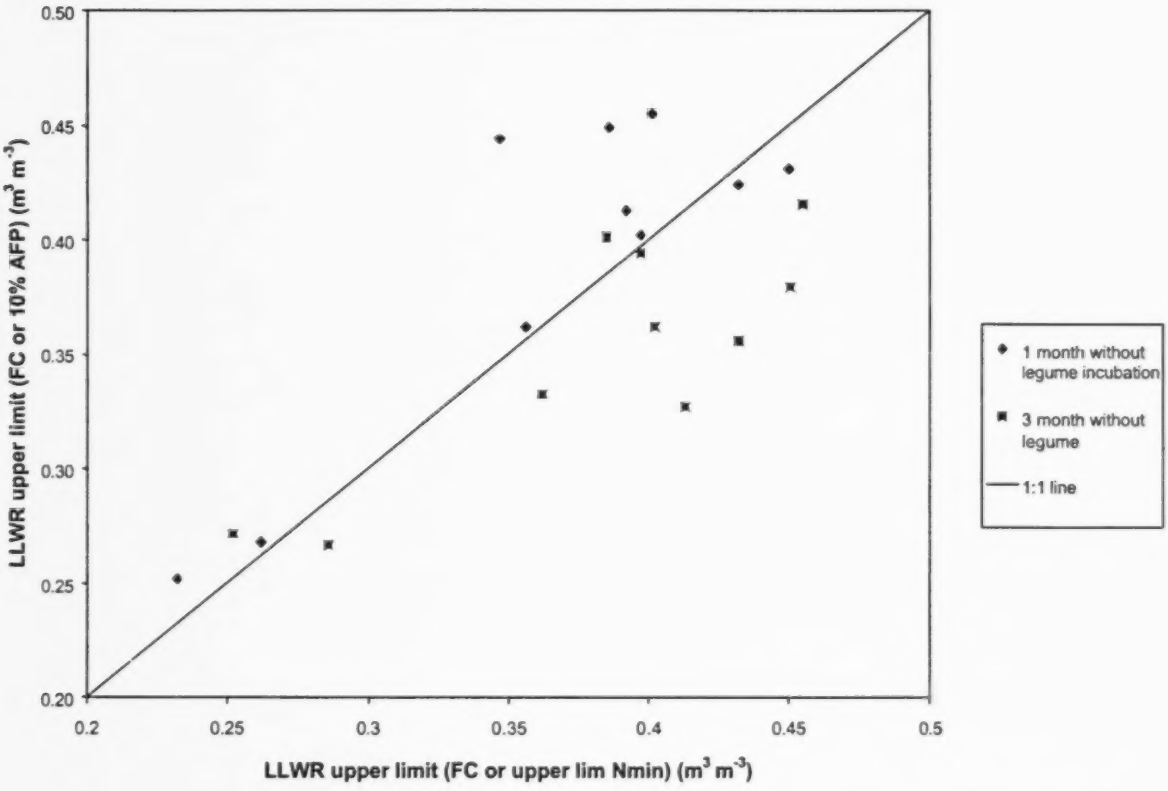
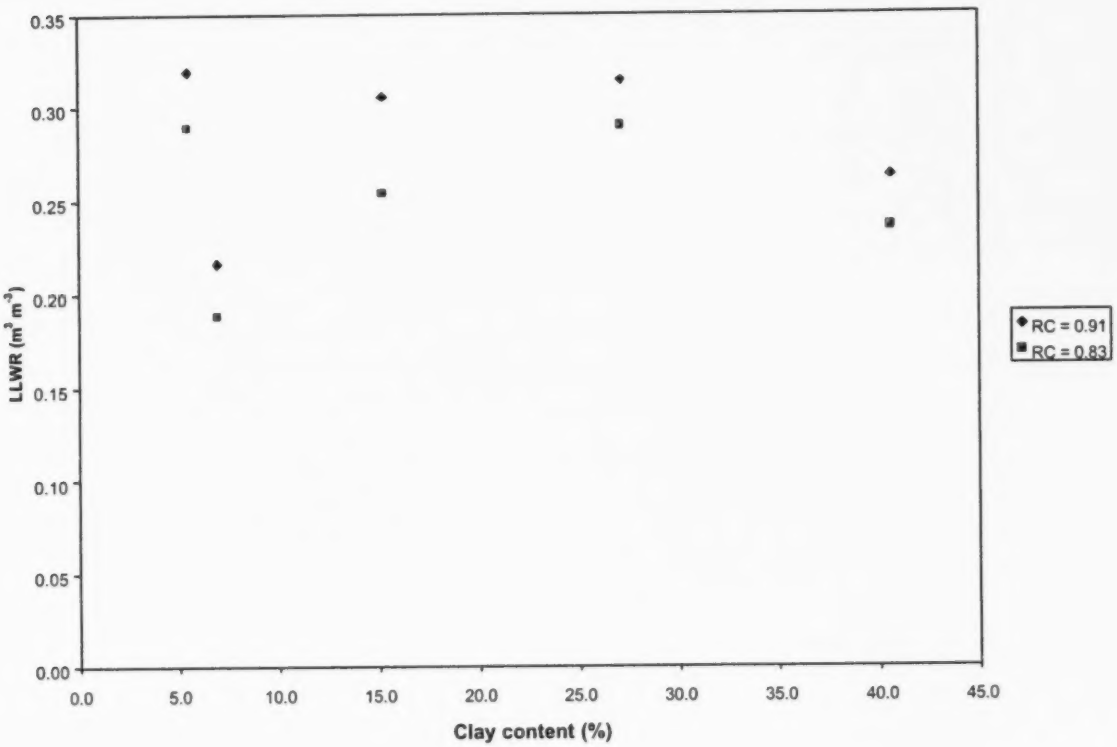


Figure 8.8 Variation in LLWR (determined from a combination of critical water contents from photosynthesis measurements and net N mineralization measurements) with clay content and relative compaction (RC).



9. Evaluation of measures of least limiting water ranges under field conditions

9.1. Introduction

Plant behavior under field conditions would be expected to differ from those in controlled environments as a consequence of differences in radiation, evaporative demand, and differences in soil structure arising from sieving the soil (creating differences in the availability of water and oxygen, and the soil resistance to penetration). Consequently, the measurements of least limiting water range for plant growth may be different in the field from those measured in controlled environments. While these differences are acceptable in a study in a study designed to improve our understanding of the complex relations between soil structure, water content and plant behavior, the applicability of conclusions from studies in controlled environments to field conditions becomes questionable if the response of hybrids to stress is not qualitatively similar under field and controlled environment conditions.

9.2. Objectives

The objective of this study was to determine if corn hybrids, grown in soil with a given structure under field conditions, respond to different levels of drought stress in a manner that is qualitatively similar to that in controlled environments. A secondary objective was to determine if corn hybrids varied in their response to fertilizer N under different conditions of drought stress.

The study was intended to be a preliminary study since funding limitations precluded the possibility of extending the study beyond one growing season or the possibility of making detailed measurements of gas exchange.

9.3. Materials and methods

Variable levels of drought stress were obtained by locating the plots on a variable landscape. The site was located at the Elora Research Station. Plots extended 156 m in length from the top to the bottom of a slope with an elevation change of 9.5 m. Previous studies had indicated a significant variation in soil water content (0-30 cm) and in corn yields across the landscape. Texture was reasonably uniform across the landscape with clay contents ranging from 14 to 16%. Organic carbon contents varied with position in the landscape. Two hybrids (Pride 5 and Pioneer 3902), two nitrogen treatments (0 and 150 kg N/ha) and four reps were established in a randomized block design (16 strips, 4 m in width). Four locations were selected

across each plot to represent different landscape locations (1, top of slope; 2, shoulder of slope; 3, back slope and 4, foot slope positions). Organic carbon contents, estimated from corresponding landscape positions on experiments located on either side of these plots were 2.33, 1.62, 1.33 and 2.00 % for locations 1, 2, 3, and 4, respectively. Samples for the N soil test (0-0.3 m) were taken on the 0N plots on June 3 prior to side dressing. Soil water content was measured weekly (0-30 cm) using TDR probes (8 probes per location). Total biomass and leaf area at silking and final grain yield were measured.

9.4. Results and discussion

The seasonal variation in soil water content to a depth of 0.3 m at the different locations on the landscape of the plots in 1998 is illustrated in Fig 9.1. The water contents followed the same pattern over time at the different locations indicating temporal stability in the spatial patterns in water content. The water contents were consistently lowest in the back slope position (loc. 3) and highest in the top of the slope (loc. 1). Statistical analyses indicated a significant ($P<0.05$) effect of location and nitrogen on water content but no effect of hybrid. No interaction terms were significant. The water content averaged across time, hybrid and location was 0.115 and 0.124 m^3m^{-3} on the +N and 0N treatments, respectively.

Biomass and leaf area measured at the time of silking (July 31) were influenced by location and hybrid but there were no statistically significant effects of N or interaction terms. The average biomass at location 1 and 3 were 7220 and 6361 kg ha^{-1}, respectively. The corresponding leaf areas were 28,000 and 24,703 m^2 ha^{-1}. Biomass of Pride 5 and Pioneer 3902, averaged across locations and N treatments were 6586 and 7600 kg ha^{-1}, respectively. Corresponding leaf areas were 25,127 and 28,936 m^2 ha^{-1}.

Final grain yields were significantly influenced by location, hybrid and a hybrid*N interaction. Yields (15.5% moisture) were lowest on the back slope position (4793 kg ha^{-1}) and highest at the top of the slope (7467 kg ha^{-1}). Yields of Pioneer 3902 were 7489 kg ha^{-1} compared to 5801 kg ha^{-1} for Pride 5. Pioneer 3902 was responsive to N, with yields increasing from 7274 to 7702 kg ha^{-1} with the additional N, whereas there were no changes in the yields of Pride 5 (5944 and 5656 kg ha^{-1}).

The lack of any significant hybrid*location or hybrid*location *N effects on biomass at silking or grain yield implies that the two hybrids did not respond differently to stresses associated with landscape position. The effect of location on biomass at silking and final grain yields would be expected to be largely related to water content in the +N treatments. Organic matter contents on this site have been found to be strongly positively correlated with seasonal average water contents; increasing organic matter contents would, therefore, coincide with

increasing mineral N which would complement the effects of water content in the 0N treatment. The small water contents at the time of silking and shortly thereafter may have had the most significant effect on yields. Correlations using seasonal average water contents or water contents measured on August 3 accounted for similar amounts of the variability in yield (as would be expected if the spatial patterns in water content are temporally stable, i.e., the patterns in water content at one time are highly correlated with those measured at another time or with the pattern of seasonal average water content). The relation between the water content on Aug 3 and yields at the four locations (individual date for reps included) on the landscape are illustrated in Figs. 9.2 and 9.3 for the +N treatment of Pride 5 and Pioneer 3902, respectively. The data of these two treatments were fitted to a logistic function which describes a curvilinear increase in yield (Y) with seasonal average water content (θ) to a maximum value and approximates the piece-wise linear fitting procedure used in Chap. 5. The following relations were obtained and are shown on the corresponding figures:

Pioneer 3902	$Y = 8443/(1+\exp((-523.1)(\theta-0.06212)))$ $R^2=0.69$	9.1
Pride 5	$Y = 6293/(1+\exp((-409.6)(\theta-0.05777)))$ $R^2=0.65$	9.2

The estimated maximum yields for Pioneer and Pride were 8443 and 6293 kg ha^{-1}, respectively. The water contents at which yields were 0.95 of the maximum (an approximation of θ_t derived in the piece-wise linear fit, chapter 5) were 0.07 m^3m^{-3} for both the Pioneer and Pride hybrids, respectively. As a comparison, values of θ_t obtained from gas exchange measurements under growth room conditions using Pioneer 3902 at the 12 leaf stage for the soil from this site was 0.19 m^3m^{-3} (Table 5.1). The water contents at which yields were 0.1 of the maximum (an approximation of θ_{ll} derived in the piece-wise linear fit, chapter 5) were 0.06 and 0.05 m^3m^{-3} for the Pioneer and Pride hybrids, respectively. The corresponding average value obtained for the Pioneer hybrid in the growth room was 0.08 m^3m^{-3}. While the absolute magnitude of the critical values of the seasonal average water contents would not be expected to be identical to those obtained under growth room conditions, the compatibility in behavior of the two hybrids under the two environments is critically important. The maximum rates of gas exchange and the maximum yields were much higher for Pioneer 3902 than Pride 5. However, the water contents at which either gas exchange or yield began to depart from the maximum value (θ_t) were similar for the two hybrids. In addition, the water contents at which gas exchange or yields approached minimum values (θ_{ll}) were similar for the two hybrids. An implication of the lack of a hybrid effect on θ_t and θ_{ll} would be that relative yields (observed yields of the two hybrids divided by their respective maximum yields, obtained from Eqn. 9.1 and 9.2) should respond similarly to

water content. Conversely, the decline in yields with decreasing water content of the two hybrids is in proportion to their maximum yields.

An obvious difference between the yield response to water content illustrated in Fig 9.2 (assuming the water stress at this stage of growth had a major influence on final yield) and the response in photosynthesis to declining water content (Fig. 5.1) is the range in water contents θ_t-θ_{ll}. The decline in yield due to drought occurred across a much narrower range in water contents than the decline in photosynthesis. While values of θ_{ll} were about the same, values of θ_t were much greater when derived from photosynthesis measurements under growth room conditions than values derived from Fig. 9.2. While this difference may reflect the ability of the plant to extract water from depths below 0.30 m, or other differences between the greenhouse and growth room environments, this difference is important in assessing the influence of soil structure and water content on yield and merits further research under field conditions.

Measurements of N in the soil and plant tissue throughout the growing season were not made as a consequence of budget limitations. Consequently, the concepts of a least limiting water range for N mineralization could not be evaluated under field conditions.

Only Pioneer 3902 responded to fertilizer N. The increase in yield with additional N (delta yield) was related to soil test N and seasonal average water content using forward stepwise regression analyses (Statsoft, 1999). The analyses gave the following relation:

$$\text{Delta yield} = -13405 - 1.113\ N^2 + 260748\ \theta - 1138600\ \theta^2 \quad R^2=0.38,\ P<0.05 \qquad 9.3$$

This relation (Fig 9.4), while not strong, indicates a decline in yield response to fertilizer N with increasing soil test N as expected, but delta N is also influenced by soil water content in a parabolic manner. For a given inorganic N level, yield response to N was least at the driest locations in the landscape (loc. 3). Increasing water content resulted in increases in delta yield to a maximum, followed by decline in delta yield at higher water contents. The decline in delta yield at the greatest water contents and a given soil test N value may have reflected a decline in yield on sites with high organic matter content that contributed supplementary inorganic N in the 0N treatment through the growing season. If so, the N soil test did not provide a measure of this supplementary N. An implication of this relation is that the N soil test and measures of soil structure and water content may not be adequate to predict delta N. A surrogate variable that incorporates an influence of soil structure, water content and potentially available N released through the growing season may be required, in addition to the N soil test. A potential surrogate

variable is organic carbon. Current studies (E. G. Beauchamp, principal investigator) are assessing this possibility across a range of landscapes in Ontario

9.5. Conclusions

The field study, although extending over only one growing season, has confirmed that the two hybrids respond similarly to drought stress as was observed in a controlled environment. Consequently, characterization of soil structure using a least limiting water range that is based on measurements of biological processes such as rates of gas exchange, would appear to be applicable to different corn hybrids.

Soil water contents reached a minimum during the silking period and this stress is expected to have had a significant influence on final grain yields. Yields were correlated with water content on Aug. 3 using a logistic function and critical water contents calculated where the yield began to decrease quickly with decreasing water content and where the yield approached zero. The lower limit was similar in magnitude to the lower limit measured in the gas exchange studies. However, the critical water content below which gas exchange rapidly decreased (θ_t) was much greater than the value below which yields rapidly decreased. Further research is necessary to determine the critical water contents for gas exchange under field conditions and the relation of these water contents to water contents that are critical to yield during yield-determining stages of plant development.

The hybrids differed in their response to fertilizer N. Pride 5 was unresponsive to fertilizer N. The yields of Pioneer 3902 responded to fertilizer N but the magnitude of the response (delta yield) varied across the landscape. Delta yield was correlated with soil test N and seasonal average water content.

9.6. References cited

Statsoft 1999. Statistica for Windows. Statsoft Inc. Tulsa, OK, USA.

Figure 9.1 Water content (0-0.03 m) at top- (loc. 1), shoulder- (loc. 2), back- (loc. 3) and foot slope (loc. 4) positions in the landscape (averaged across N and hybrid treatment) through the 1998 growing season.

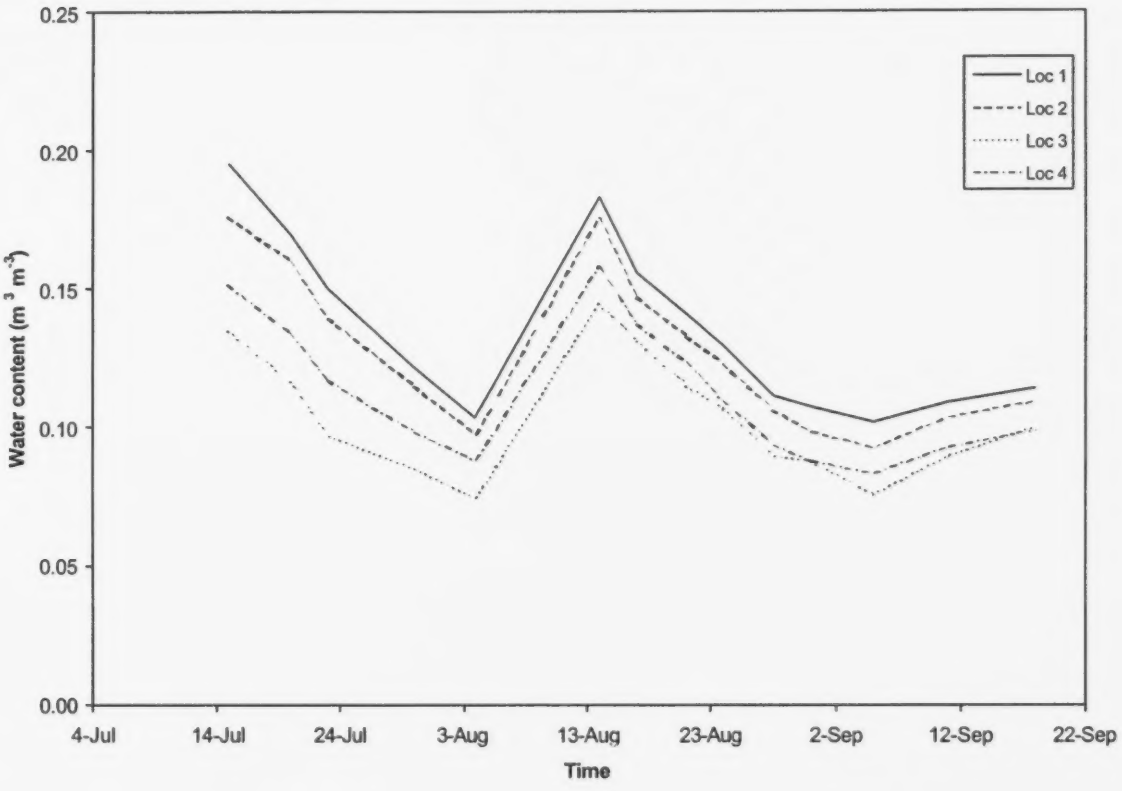


Figure 9.2 Grain yield as a function of water content on Aug 3 at the four locations on the landscape for Pride 5 a N treatment of 150 kg ha^{-1}

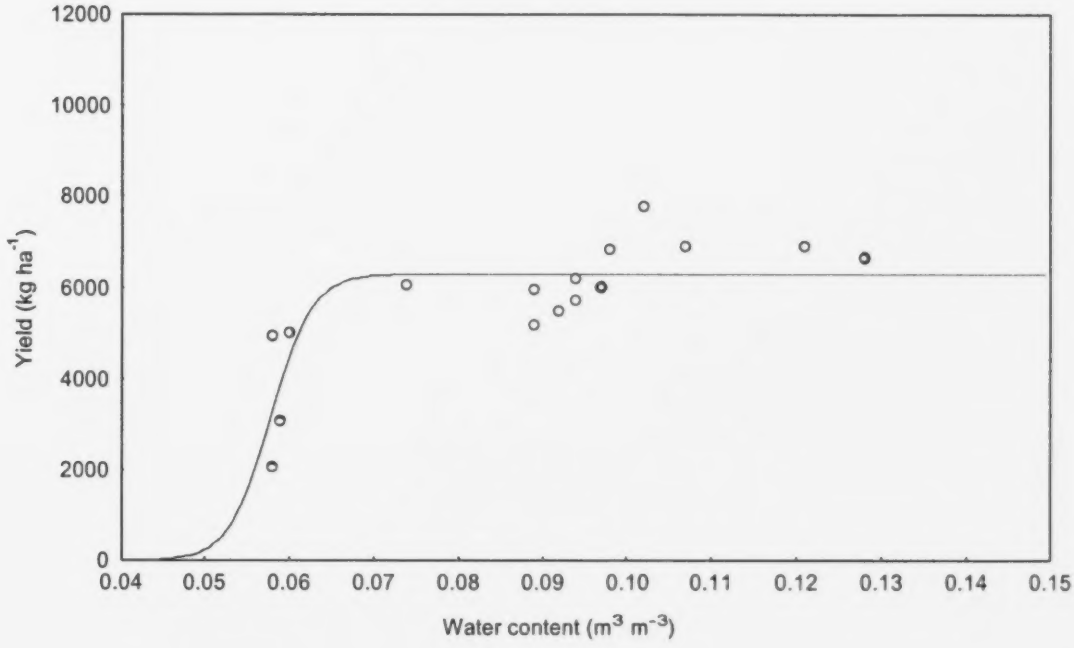


Figure 9.3. Grain yield as a function of water content on Aug 3 at the four locations on the landscape for Pioneer 3902 and a N treatment of 150 kg ha^{-1}

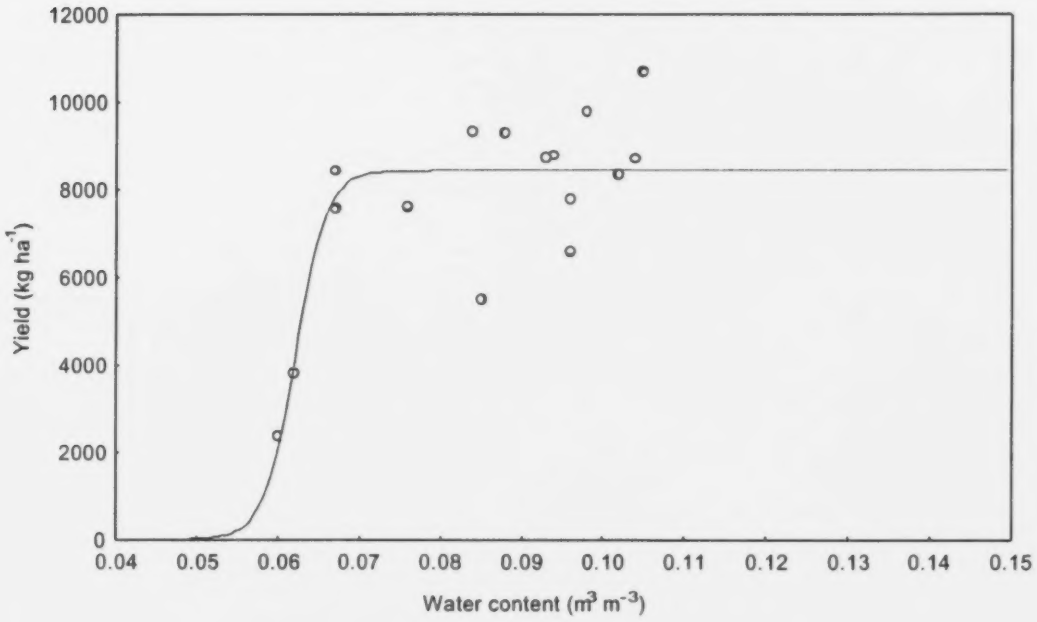
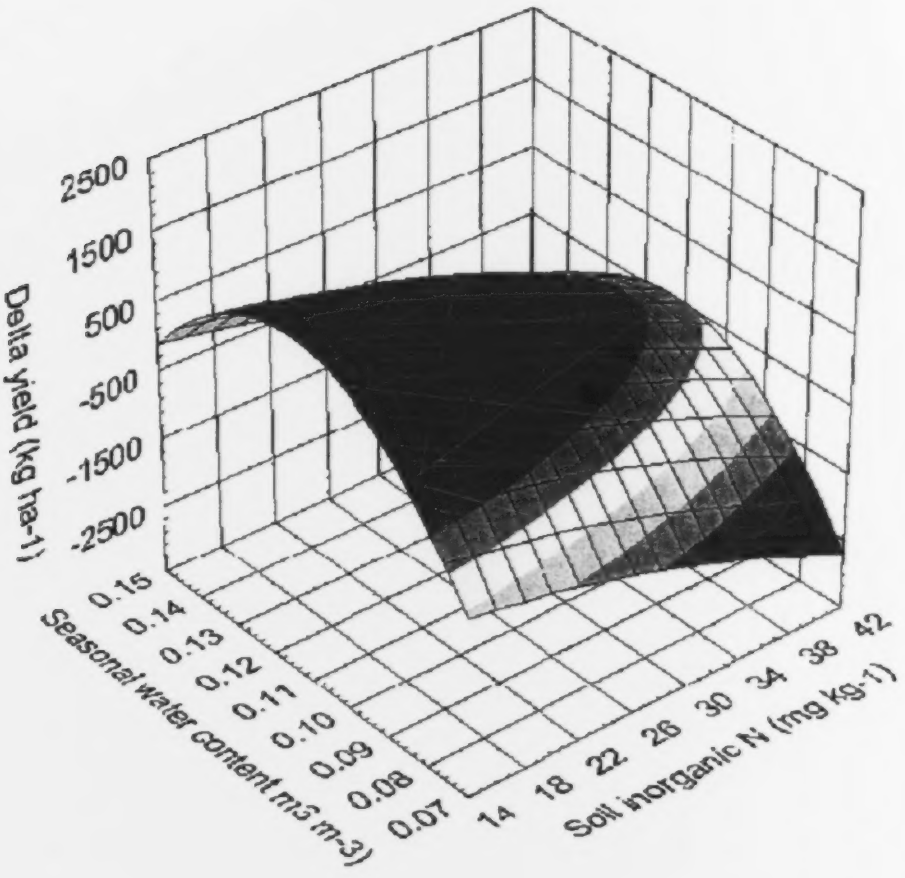


Figure 9.4 Variation in yield response to the application of 150 kg N ha^{-1} (delta yield) with soil test N and seasonal average soil water content.



10. General conclusions and future directions

The growth room studies of gas exchange rates of two different corn hybrids, incubation studies of net N mineralization of soil organic N and legume N and the preliminary field study of the variation across a landscape in yield response of the two hybrids to fertilizer N have illustrated the value of characterizing soil structure and water regimes in terms of critical soil water contents. These critical water contents can be used to define ranges in water contents that are non- or least limiting to essential biological processes (e.g., photosynthesis by plants, net N mineralization by microorganisms). The studies have yielded the following conclusions.

- Two critical water contents were defined for gas exchange processes in plants as soil drying occurred under growth room conditions, one at which gas exchange began to fall rapidly from the maximum rates of gas exchange (θ_t), and one at which gas exchange approached zero (θ_{ll}). Values of θ_t defined the lower limit of a non-limiting water range, whereas values of θ_{ll} were taken as the lower limit of the least limiting water range. Neither of the two critical water contents occurred at values of water potential or soil resistance to penetration that have characteristically been assumed to be limiting. Values of θ_t appeared to be most closely associated with water contents at which further loss in water resulted in a rapid increase in soil resistance to penetration and/or a rapid decrease in water potential. Values of θ_{ll} in the coarsest textured soils coincided with a water potential of -1.5 MPa and a small soil resistance to penetration whereas in the finer textured soils θ_{ll} coincided with a soil resistance to penetration of about 7 MPa and a large water potential (small soil water suction). Values of θ_{ll} for soils of intermediate texture did not coincide with characteristic values of either water potential or soil resistance. We conclude that the lower limit of the least limiting water range for gas exchange cannot be readily predicted from the soil water release curve and the soil resistance curve by applying specific limits of -1.5 MPa potential or 2 MPa soil resistance, as previously assumed. Both of the critical water contents were strongly correlated with clay and organic carbon contents, and these correlations will be particularly useful in predicting the limits from readily measurable soil characteristics. However, the correlations provide little information on causal mechanisms.

- Values of θ_t and θ_{ll} did not vary with hybrid but θ_{ll} did vary slightly with stage of plant development (values of θ_{ll} increased from the 12-leaf stage to grain filling).

- A critical water content could not be identified for gas exchange in plants as soil water contents increased to saturation. The response of plants to large water contents varied with the stage of development. Rates of gas exchange of plants at the silking and grain filling stages were not influenced by saturating the soil for 10 days. At the 15-leaf stage, the impact of saturating the soil on gas exchange was time-dependent. Redox potential declined continuously over time under saturated conditions, whereas the rates of photosynthesis remained constant until the redox potential fell below a critical threshold value. The threshold values ranged from 97 to 237 mv and varied with soil and hybrid. Identification of a critical water content at which the redox potential would fall to the threshold redox potential (within a set time period) could be used in conjunction with θ_l to define a non-limiting water range for plant growth. Extrapolating the relations between photosynthesis and redox potential to a rate of photosynthesis of zero gave values of redox potential ranging from -135 to-64 mv. Following the same logic to define an upper limit for a non-limiting water range, the water contents at which the redox potential fell to a value causing photosynthesis to cease might be used in conjunction with θ_{ll} to define an upper limit of the least limiting water range.

- Evidence was not found to support the commonly held assumption that rates of gas exchange, plant development and N uptake are the same for plants growing in soils with different structure where conventional measurements of the supplies of water and oxygen and soil resistance to penetration indicate these factors are not limiting. Instead, gas exchange rates, rate of plant development and N uptake were found to vary among soils and were strongly negatively correlated with clay content. The mean weight diameter of aggregates was positively correlated with clay content which resulted in a strong negative relation between aggregate diameter and gas exchange rates, rate of plant development or N uptake. The reason(s) for these relations could not be determined.

- Critical water contents for net N mineralization were identified. The lower critical water content coincided with the water content at which there was had been no net increase in inorganic N above the initial level after incubating soil for 1 or 3 months. This limit was found to be similar or lower than the lower limit for gas exchange in corn. This implies that the demand for N by the crop would reach minimum values (assuming the variation with soil water content in plant growth and N demand parallel that of gas exchange) at water contents equivalent to, or greater than that at which net N mineralization is zero. The upper critical water content coincided with the water content at which denitrification reduced the inorganic N level to the initial level after incubating soil for 1 or 3 months. The upper critical water contents increased with soil compaction and duration of

incubation. The upper critical water contents could not be predicted from air-filled pore space, a variable often used to estimate the onset of anaerobic conditions. The upper limit was less than the water content at field capacity in several soils indicating that significant losses of N would occur in these soils, through denitrification, after rapid drainage had ceased.

- In the absence of a well-defined upper limit of water contents for gas exchange, the upper limit for net N mineralization was used in conjunction with the lower limit for gas exchange to define a least limiting water range (LLWR) for plant growth. This estimate of the LLWR implies that plant growth at the lower end of the range is limited by physical constraints (water supply or soil resistance to penetration) and at the upper end by inadequate N supply. The LLWR varied parabolically with clay content and, at low clay contents, increased with organic carbon.

- The most extensive drought occurred during the silking period in the preliminary field study. Stress experienced by the crop in that period was expected to have had a strong influence on final grain yield. Non-linear regression techniques were used to relate yields to soil water content at that time and critical water contents calculated in a similar manner to that used in the gas exchange studies in the growth rooms. The lower limit was similar in magnitude to that determined under growth room conditions. The field study confirmed results found in the growth room study that the critical water contents did not vary with hybrid.

- The yield response to N was different for the two hybrids with the lower yielding Pride 5 exhibiting no response to an application of 150 kg N ha^{-1}. The yield response of Pioneer 3902 varied across the landscape in response to variation in soil test N and the seasonal average soil water content.

This study has conclusively illustrated the need to unravel the complex relations between soil structure, soil water content, N dynamics, photosynthesis and transpiration in order to improve then efficiency of fertilizer N use. Future studies need to be directed first to additional growth room studies, then to controlled environments in the field and finally to field-scale studies.

Future studies under growth room conditions should answer questions that are critical to understanding the fundamental definition of the least limiting water ranges. In the case of the LLWR for plant growth, research should focus on the following questions:

- In the case of the lower limit,
  - how do the combination of limiting values of water potential and soil resistance to penetration define the critical water content in soils with different structural characteristics and
  - is the interaction between limiting potential and soil resistance influenced by N levels?
- In the case of the upper limit,
  - why do the redox potentials that are critical threshold values for photosynthesis vary among soils,
  - can a critical water content be identified in soils of different structure at which the redox potential falls to the threshold value within an arbitrary time period, say 4 days, and if so, can the critical water content be predicted from readily measurable soil characteristics,
  - how does this water content compare to the water content at which net mineralization falls to zero (temperature is assumed to be constant)?
- Why do gas exchange rates vary with clay content (or aggregate diameter) under conditions that aeration, water potential and soil resistance to penetration are ostensibly non-limiting (the answers to this question may also help us understand the causes of reduced early growth of corn under no-till conditions, particularly on fine textured soils)?

In the case of a LLWR for net mineralization, research should focus on the following questions.

- How does net mineralization change with time after a change in water content (an upper limit to the LLWR is most relevant to field conditions if the net mineralization changes in concert with changes in water content)?
- Why does the upper limit of net mineralization increase with soil compaction?
- Are the upper and lower limits influenced by the presence of a growing plant?

The growth room studies need to be extended to controlled environments under field conditions to assess the influence of radiation levels, evaporative demand and different soil N levels on the critical water contents for gas exchange during both soil drying and wetting to saturation. Particular attention should be given to θ_t, determination of threshold redox potentials and water contents at which these redox potentials are reached within a given time, as well as redox potentials at which gas exchange approaches zero and the corresponding critical water contents.

Finally, studies must be undertaken across a range of soils to determine the most effective manner of combining data on the LLWR with N soil test data to increase the accuracy of estimates of fertilizer-N requirements.

Appendix 1. Acronyms used in report

FP: air-filled porosity
FDL: free drainage limit
LLWR: least limiting water range
NUE: nitrogen use efficiency
OC: organic carbon
PAW_t: fraction of TTW remaining in soil at θ_t
PPFD: photosynthetic photon flux density
θ: volumetric water content
θ_{fdl}: volumetric water content at free drainage limit
θ_t: threshold volumetric water content (gas exchange begins to decrease if water content decreased
θ_{ll}: lower limit of least limiting water range, rates of gas exchange at this water content approach zero
RC: relative compaction
T_p: daily rate of transpiration per pot
$T_{p\ pot}$: Maximum daily rate of transpiration per pot
TTW: total transpirable water, θ_{fdl}-θ_{ll}
WFPS: water-filled pore space